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CONTENTS

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(WITH 4 FIGURES)

In the past it has been customary to treat all, or nearly all, of the small, operculate discomycetes with conspicuous hairs as members of a single large genus under the name *Lachnea* (Gillet **1879**, Saccardo **1889**, Phillips **1887**, Massee **1895**, Rehm **1896**, Svrček **1948**) or *Patella* (Morgan **1902**, Seaver **1928**). More recently some authors (Le Gal **1953**, Kanouse **1958**), feeling the need to recognize the diversity that exists within the group, have turned to the re-examination of the generic concepts suggested by the brilliant work of Boudier (**1885**). The present paper is a contribution to the latter trend. It attempts to establish the validity of the genus *Scutellinia* (Cke.) Lambotte (= *Ciliaria* Boudier 1885) and designate its limits. Although a number of species are described, including those most commonly collected in eastern North America, this paper does not constitute a comprehensive monograph even of those species occurring in North America.

The writer wishes to thank the following individuals and their respective institutions for their cooperation in loaning specimens or providing information about specimens in their collections: Dr. Donald P. Rogers and Dr. Clark T. Rogerson, New York Botanical Garden; Miss

[1] Based in part on a thesis presented in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Cornell University.

[2] Present address: Department of Biology, Swarthmore College, Swarthmore, Pennsylvania.

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Edith K. Cash and Mr. John A. Stevenson, National Fungus Collections, Beltsville; Dr. C. Earle Smith, Philadelphia Academy of Natural Sciences; Dr. George T. Jones, Oberlin College, Oberlin, Ohio; Dr. John F. Davidson, University of Nebraska, Lincoln, Nebraska; Sir Edward Salisbury, Royal Botanic Gardens, Kew; Dr. A. Kalela and Mr. N. Malmström, Botanical Museum, Helsinki; Prof. Dr. Frantisek A. Novak, Botanical Institute of the Charles University, Prague; Dr. E. Hulten, Naturhistoriska Riksmuseum, Stockholm; Prof. Sir William W. Smith, Royal Botanic Garden, Edinburgh; Dr. H. J. Maresquelle, Institut de Botanique de la Faculté des Sciences de Strasbourg.

He wishes also to express his gratitude to Dr. William Dress of the Bailey Hortorium, Cornell University, for his assistance with the Latin diagnoses. Finally, the writer wishes to acknowledge a great debt of gratitude to Dr. Richard P. Korf, Dept. of Plant Pathology, Cornell University, under whose supervision much of this work was done.

MORPHOLOGY OF THE ASCOCARP

The morphology of the ascocarp of all species of *Scutellinia* is remarkably similar. The published anatomical descriptions of *Scutellinia scutellata* (Durand **1900**, Lagarde **1908**, and Corner **1929**) serve equally well for any other species of the genus.

A vertical section through an apothecium (FIG. 1A) reveals the following features. First, lining the cup, is a hymenium of nearly cylindrical asci interspersed with, and exceeded by, narrowly clavate paraphyses whose yellow to red carotenoid pigments (Heim **1947**: 104) give the hymenium its characteristic color. Below the hymenium a subhymenium of small-celled ascogenous hyphae merges without a distinguishable boundary into a medullary excipulum of larger *textura prismatica* cells elongated in the horizontal axis. To the outside an ectal excipulum of much larger *textura globulosa* to *textura porrecta* cells, with long axes oriented radially from the center of the cup, envelops the rest of the apothecium and rises above the hymenium at the sides to form a distinct margin. In apothecia from soil the more fragile cells of the ectal excipulum are frequently damaged in collecting or sectioning. Nevertheless, the layer is readily demonstrated in all species. The final, and perhaps most striking, feature of the apothecium is the fringe of long, dark, heavy-walled hairs that originate in the medullary excipulum and project, bristle-like, through the ectal excipulum to the outside. These hairs have been discussed by a number of authors (Massee **1897**: 231, Gwynne-Vaughan and Williamson **1933**: 380, Le Gal **1953**: 117) and deserve further attention here.

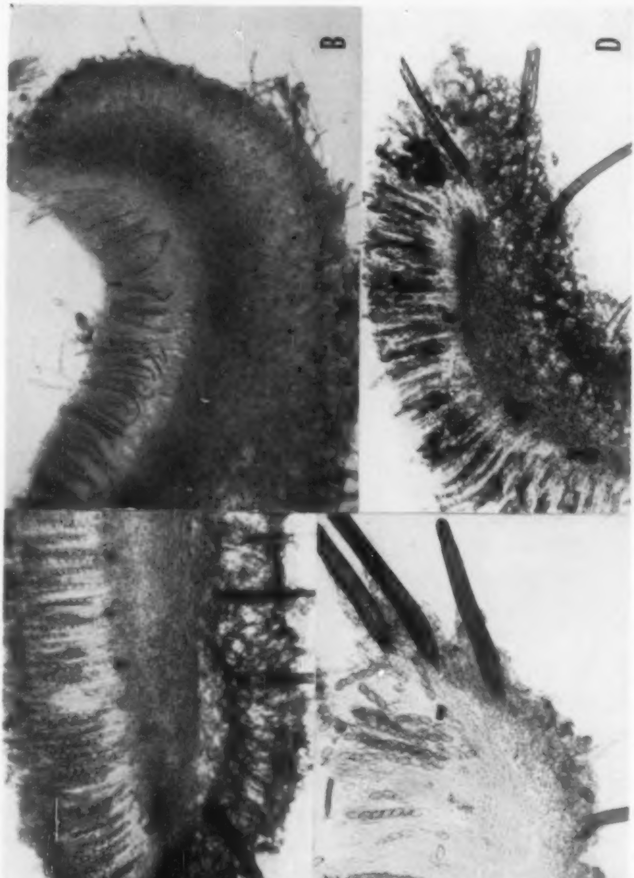

FIG. 1, A–D. Freehand sections of apothecia. A. *Scutellinia scutellata*, × 60. B. *Melastiza charteri*, × 60. C. *Scutellinia asperrima*, from holotype, × 95. D. *Scutellinia asperrima*, from holotype, × 60.

There are actually two distinct types of hair-like projections from the exterior of the apothecium: thin-walled, hyaline, hypha-like extensions of the external cells of the excipulum, hereafter referred to as superficial hairs, and the heavy-walled bristles mentioned above, which will be called rooting hairs. Superficial hairs are found in varying abundance throughout the genus *Scutellinia* and in a large number of other genera as well. Rooting hairs, on the contrary are abundant in all species of *Scutellinia* but in no other genus, except the closely related one, *Cheilymenia.*

It is not necessary to section an apothecium in order to recognize these rooting hairs, for they have another characteristic that is readily discernible even in preparations of crushed apothecia (FIG. 3B, 3D). The base of the hair is divided in such a way that it appears to have a number of points of origin. The ontogeny of these hairs has been described (Massee **1897**: 231) as analogous, or even homologous, to the development of asci from croziers. That the process is at least somewhat more complex than that is indicated by the fact that although hairs with bifurcate bases are common, others with three, four, five, or even more divisions are to be found in nearly every apothecium.

Another feature of these hairs, hitherto unreported, was brought to the writer's attention by Dr. R. P. Korf. In some instances the largest hairs of an apothecium are found to have smaller, but otherwise typical, hairs growing inside them (FIG. 3A, 3C). This phenomenon has been seen repeatedly throughout the genus. It appears to be associated with damage of the larger enclosing hair.

ASCOSPORES

Unlike the apothecia, which are remarkably similar in structure in all species, the ascospores of different species of *Scutellinia* exhibit a marked amount of variability. Their shape ranges from elongate-ellipsoid or subfusiform (FIG. 4E) to spherical (FIG. 4B) and surface sculpturing may take the form of a heavy reticulum (FIG. 4C), spines (FIG. 4A), or warts (FIG. 4H) or even be completely absent (FIG. 4G). The sculpturing, where present, is of a callose-like material which stains when heated in cotton blue (Le Gal **1947**). When young the spores of all species contain a number of small guttules which coalesce to form one to several larger ones at maturity.

OCCURRENCE

Scutellinia is a highly cosmopolitan genus, occurring on every continent and from the tropics to the arctic wherever there is sufficient local

moisture. In this hemisphere it is known from the Bering Straight through to the Canal Zone and into Argentina.

The genus may be found on a variety of non-living organic substrates, rotting wood and soil being the most common. Its occurrence on dung has been reported (Seaver **1928**) but, in this country at least, is a rare phenomenon. Among the more unusual substrates mention might be made of several collections from sporophores of *Polyporus betulinus* and *Ganoderma applanatum*.

In northern North America apothecia may be found from late April through November but in the tropics fruiting apparently occurs throughout the year.

RELATED GENERA

As treated in this paper the genus *Scutellinia* is characterized by the possession of rooting hairs; orange to red carotenoid pigments localized in the paraphyses; a pseudoparenchymatous ectal excipulum; and ellipsoid to globose, guttulate, sculptured (rarely smooth) ascospores. This incorporates species formerly placed in the genera *Melastiza, Sphaerospora,* and *Trichophaea* in addition to those species generally grouped with *Scutellinia scutellata*.

Seaver (**1928**) included *Melastiza pennsylvanica* Seaver and *Melastiza asperrima* (Ell. & Ev.) ex Seaver in the genus *Melastiza* Boud., presumably because of the reticulate sculpturing of the ascospores. Unlike the type of the genus *Melastiza, M. charteri* (FIG. 1B), both *M. pennsylvanica* and *M. asperrima* possess the excipular structure and rooting hairs typical of *Scutellinia scutellata* (see FIGS. 1C, 1D). As for the reticulately sculptured spores, close examination of stained material reveals that whereas the sculpturing in *M. asperrima* forms a reticulum (FIG. 4C), in *M. pennsylvanica* (FIG. 4D) it consists of branched ridges and crests which commonly fail to interconnect. *M. pennsylvanica* and *M. asperrima* should be transferred to the genus *Scutellinia*.

The type of the genus *Sphaerospora* Sacc., *Peziza trechispora* Berk. & Br., also exhibits the apothecial structure (FIGS. 2C, 2D), pigments, and rooting hairs (FIG. 3B) of *Scutellinia scutellata*, differing only in the shape of its ascospores, which are spherical. By contrast, most of the other species included by Saccardo and subsequent authors in the genus *Sphaerospora* have excipular tissues, hairs, pigments, etc., of quite a different character (see FIG. 2B). This suggests that *Peziza trechispora* should be included in the genus *Scutellinia* and that the affinities of the remaining species of "*Sphaerospora*" be sought elsewhere.

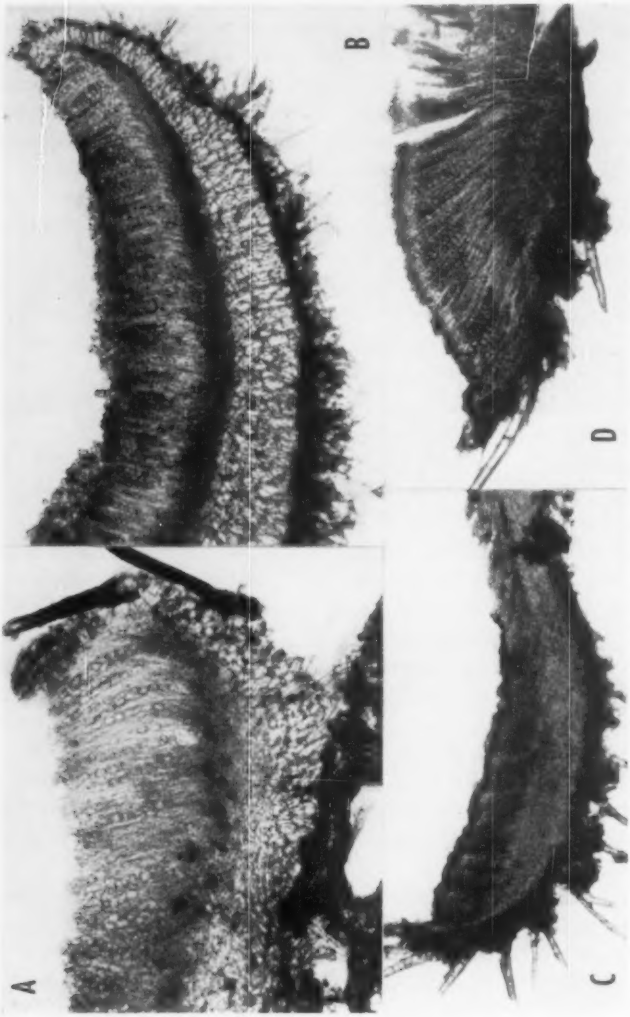

FIG. 2, A–D. Freehand sections of apothecia. A. *Scutellinia crinaceus*, ×95. B. "*Sphaerospora*" *brunnea* sensu Seaver, ×60. C & D. *Scutellinia trechispora*, from lectotype, ×60.

Le Gal (**1954**: 166) placed *Peziza erinaceus* Schw. in the genus *Trichophaea,* considering it to be intermediate in position between *Trichophaea* and *Scutellinia* because of its "almost white" hymenium and rooting hairs (FIGS. 2A, 3D). In fresh condition, however, *Peziza erinaceus* has an orange hymenium with pigments that turn blue in sulphuric acid. In all species of *Scutellinia* the pigments commonly fade rapidly on drying, so that it is not surprising that the type specimen has a hymenium which is indeed "almost white." It is the writer's belief that *Peziza erinaceus* Schw. belongs in the genus *Scutellinia.* He is supported in this belief by Dr. Kanouse (**1958**) in her recent treatment of the genus *Trichophaea.*

The genera of operculate discomycetes which have been confused with *Scutellinia* are those having small, brightly colored (yellow to red) apothecia [3] or those having conspicuous apothecial hairs.[4] Of these, only the genus *Cheilymenia* possesses rooting hairs of the type found in *Scutellinia. Cheilymenia* is in turn most readily separated from *Scutellinia* on the basis of its ascospores. The ascospores of *Cheilymenia* are unsculptured and without guttules. Moreover, the outermost layer frequently separates and floats as a loose sheath or envelope about the spore. In *Scutellinia* the spores are always guttulate and the outermost layer, which is sculptured in all of our species except *S. erinaceus,* remains attached to the spore.

THE GENERIC NAME SCUTELLINIA

The name *Scutellinia* was first employed by Cooke (**1879**: 260) as a subgenus of *Peziza,* and was raised to generic rank by Lambotte (**1887**: 299). The lectotype species of the genus is *Scutellinia scutellata* (L. ex Fr.) Lambotte (vide Le Gal, **1954**: 115).

This species has been designated the type of several other genera which deserve mention here. The name *Lachnea,* used by Fries as a subgenus of *Peziza* and raised to generic rank by Gillet (**1879**: 57), is a later homonym of *Lachnea* L. 1753 (= *Lachnaea* L. 1762), a group of flowering plants. The name *Ciliaria* Boudier (**1885**: 105) is likewise a latter homonym of a genus of flowering plants, *Ciliaria* Haworth 1821. The names *Humariella* Schröter 1893, *Patella* Weber ex Morgan 1902, and *Stereolachnea* von Höhnel 1917 are, of course, too recent to affect the status of *Scutellinia* (Cooke) Lambotte 1887.

The genus *Humaria* Fuckel (**1870**: 321) presents a problem of a

[3] *Melastiza, Cheilymenia, Coprobia, Anthracobia, Lamprospora,* etc.

[4] *Trichophaea, Humaria, Tricharia, Jafnia, Leucoscypha,* etc.

different sort. The genus was erected to include a number of setose discomycetes, among them *Peziza scutellata* L. ex Fr. and *Peziza hemisphaerica* Weber ex Fr. The writer has been unable to find in the literature any effective designation of a type species of this genus. He wishes therefore, to designate *Peziza hemisphaerica* Weber ex Fr. the LECTOTYPE species of *Humaria* Fuckel. *Mycolachnea* Maire (**1937**: 24), which is based on the same type species, thus becomes a synonym of *Humaria* Fuckel.

The present treatment includes within the genus *Scutellinia* the species *Peziza trechispora* Berk. and Br., which is the type species of two other genera, *Sphaerospora* Sacc. (**1889**: 188) and *Sphaerosporula* Kuntze (**1898**). Both of these names are more recent than, and therefore become synonyms of, *Scutellinia* Lambotte **1887**.

GENERIC DIAGNOSIS

SCUTELLINIA (Cooke) Lambotte emend. Denison [5]

Peziza subg. *Scutellinia* Cooke, Mycographia 260. 1879.

≡ *Ciliaria* Boudier, Bull. Soc. Myc. Fr. **1**: 105. 1885.

≡ *Scutellinia* (Cooke) Lambotte, Flore Myc. Belge Suppl. 299. 1887.

≡ *Humariella* Schröter, Krypt.-Fl. Schles. $\mathbf{3}^2$: 36. 1893.

≡ *Patella* Weber ex Morgan, Jour. Myc. **8**: 187. 1902.

= *Sphaerospora* Saccardo, Syll. Fung. **8**: 188. 1889.

≡ *Sphaerosporula* Kuntze, Rev. Gen. Plant. $\mathbf{3}^3$: 530. 1898.

= *Stereolachnea* von Höhnel, Ann. Myc. **15**: 353. 1917.

Apothecia small to medium sized, 1–25 mm broad, solitary to gregarious, at first subglobose and nearly closed, at maturity becoming concave, discoid, or slightly reflexed, sessile, externally clothed with hairs; excipulum of two layers: 1) the medullary excipulum continuous with the hypothecium, of small cells with their long axes horizontal, and 2) the ectal excipulum of larger, more loosely aggregated cells with their long axes oriented radially from the center of the cup, not bounded by an external, epidermis-like membrane; hymenium at maturity shallow cup-shaped to slightly reflexed, red to orange, rarely almost yellow, the pigments not developing in the absence of light, fading on drying to white or buff; rooting hairs originating in the medullary excipulum and projecting through the ectal excipulum, divided once to several times at the base, appearing to have several points of origin, broadest just above

[5] Throughout the paper the following convention has been adopted in lists of synonymy: = means a taxonomic synonym; ≡ means an obligate nomenclatural synonym.

the base, 15–40 μ, and tapering gradually to a pointed, rarely almost blunt, apex, 75–2500 μ long, dark brown, appearing black except under the microscope, rarely paler, stiff, thick-walled, and bristle-like, septate, straight, slightly curved, or crooked, simple, rarely branched; superficial hairs arising from superficial cells of the ectal exciplum, 5–20 μ broad, scarcely tapered, blunt, 50–300 μ long, hyaline to pale brown, thin-walled, septate, flexuous; asci cylindrical, 10–30 × 200–350 μ, eight-spored, arising from croziers, the apex not bluing in iodine; ascospores spherical to subfusiform or sublunate, 13–35 μ long, smooth or sculptured, hyaline to pale yellow, when immature filled with small guttules that fuse to form one or two large guttules at maturity; ascospore sculpturing rarely absent, of callose-pectose material that stains in cotton blue, developing as minute warts that remain distinct, anastomose slightly, or fuse to form a reticulum; paraphyses narrowly clavate to subfusiform, exceeding the asci, simple or somewhat branched below, when fresh containing orange carotenoid pigments that turn blue in sulphuric acid and green in iodine.

Habitat: saprophytic on rotting wood, bark, soil, charcoal, dung, or organic debris throughout the growing season.

TYPE SPECIES: *Peziza scutellata* L. ex Fr.

KEY TO INCLUDED SPECIES [6]

1. Spores spherical, strongly sculptured; apothecia occurring on soil 2
1. Spores ellipsoidal, rarely sublunate, sculptured or smooth; apothecia on soil, wood, debris, charcoal, or dung 3
   2. Spores 14–20 μ broad; spore sculpturing consisting of pyramidal warts, commonly higher than broad, with pointed or truncated apices .... *Scutellinia armatospora*
   2. Spores 20–25 μ broad; spore sculpturing consisting of rounded warts, seldom as high as broad .... *Scutellinia trechispora*
3. Spores smooth; hymenium orange to yellow; hairs short, 150–600 μ long 4
3. Spores sculptured; hymenium red to orange; hairs short or long 5
   4. Apothecia on wood, small, 2–4 mm broad, gregarious .... *Scutellinia crinaceus*
   4. Apothecia on dung or soil .... see the genus *Cheilymenia*
5. Spore sculpturing exceeding 1 μ in height, anastomosing freely to form a partial or complete reticulum 6
5. Spore sculpturing less than 1 μ in height or, if more, consisting of distinct warts not forming a reticulum 7
   6. Spore sculpturing forming an incomplete and irregular reticulum; spores 16–19 μ long .... *Scutellinia pennsylvanica*
   6. Spore sculpturing forming a complete and regular reticulum, often prolonged at the poles and thus resembling apiculi; spores 19–23 μ long .... *Scutellinia asperrima*

[6] Spore measurements do not include the thickness of sculpturing.

7. Marginal hairs short 100–700 μ long; spore sculpturing composed of large isolated warts; apothecia on soil 8
7. Marginal hairs longer, a few at least 1000 μ long; spore sculpturing consisting of numerous small warts barely visible in optical section and anastomosing freely; apothecia usually on wood, less often on a wide variety of other substrates .... *Scutellinia scutellata*
   8. Spores elongate-ellipsoid, 9–11 × 19–22 μ; spore sculpturing consisting of large truncate warts towards the poles and smaller rounded ones at the equator .... *Scutellinia verrucipolaris*
   8. Spores broadly ellipsoid, 12–15 × 18–23 μ; spore sculpturing consisting of moderate to large rounded warts distributed evenly over the surface of the spore .... *Scutellinia umbrarum*

ACCEPTED SPECIES

Scutellinia armatospora Denison sp. nov. FIG. 4A

Apothecia minuta, 2–7 mm lata, solitaria vel sparsa, orbicularia vel patellaria, late sessilia, thecio aurantiaco-rubro; pili radicati abundantes, atrobadii, breves, 75–250(–400) μ longi, septati, recti vel subcurvati, pili superficiales nulli vel inconspicui; asci subcylindrici, 20–25 × 250–300 μ, octospori; sporae globosae, (13–)14–19(–21) μ latae, distincte verrucoso-aculeatae, maturae guttula magna impletae, verrucis acute vel obtuse conicis, 1.0–2.5 μ altis, basi 0.5–1.5 μ latis; paraphyses basi 1.5–2.5 μ crassae, sursum sensim ad 6–10 μ incrassatae, ad apicem saepe subito angustatae; plantae rariores, terrestres, mensibus Julio Augustoque vigentes.

Apothecia small, 2–7 mm broad, solitary or scattered, discoid to shallow cup-shaped, closely appressed to the soil; hymenium "Spectrum Red" [7] to "Grenadine Red"; rooting hairs abundant, dark brown, short, 75–250(–400) μ, septate, straight or slightly curved; superficial hairs absent or inconspicuous; asci subcylindrical, 20–25 × 250–300 μ, eight-spored; ascospores spherical, (13–)14–19(–21) μ broad, at maturity uniguttulate, strongly sculptured; ascospore sculpturing [8] consisting of great spine-like warts up to 2 μ high, 0.5–1.5 μ broad at the base, tapering upward, sometimes with a pointed apex, often forming a truncated pyramid, distinct, showing little or no tendency to anastomose; paraphyses clavate to subfusiform, 1.5–2.5 μ broad below, swelling to 6–10 μ broad just below the apex, frequently narrowing again abruptly at the extreme apex.

Habitat: On soil, July to August, rare.

Name: From Latin *armatus* = armed, and Latin *spora* = seed; named for the spine-covered spores.

[7] Names of colors enclosed in quotation marks refer to the corresponding color chip in Ridgway (**1912**).

[8] Descriptions and measurements were made from spores mounted in cotton blue in lactic acid (vide Le Gal **1947**, Korf **1952**).

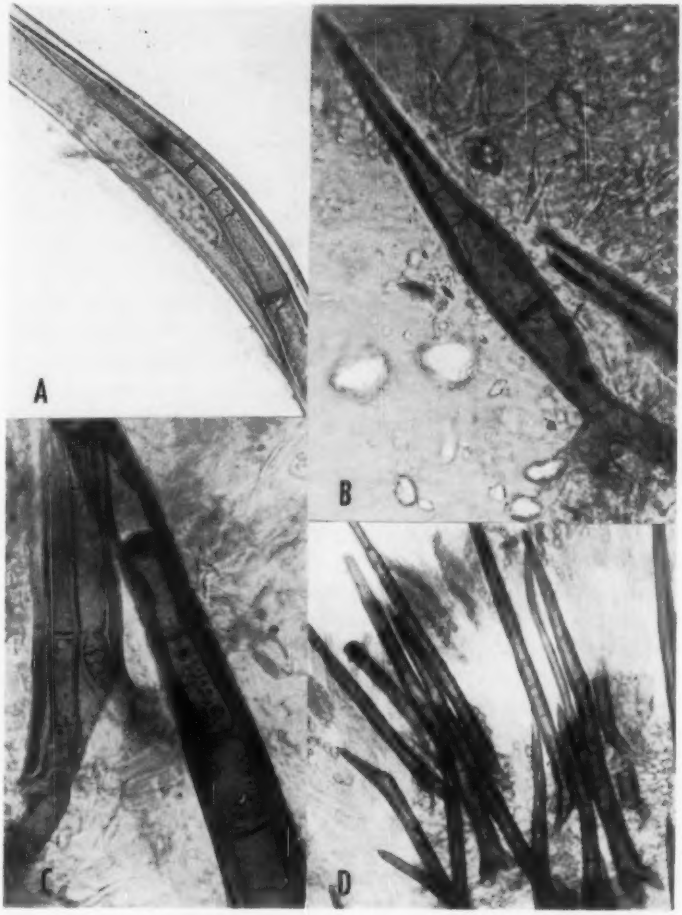

FIG. 3, A–D. Apothecial hairs. A & C. *Scutellinia* spp. showing hairs within hairs, × 450. B. *Scutellinia trechispora*, × 450. D. *Scutellinia crinaceus*, from holotype, × 90.

Type locality: Canandaigua, New York.
Type specimen: in CUP.[9]

[9] The abbreviations of herbaria used are those proposed by Lanjouw & Stafleu (**1956**) with the following additions: CUP-D = Durand Herbarium, Dept. of Plant Pathology, Cornell University; RPK = the personal herbarium of Dr. R. P. Korf; WCD = the writer's herbarium.

Illustrations: Boudier, Icones Myc. **2**: *Pl. 378.* 1906 (*Ciliaria asperior*); Gillet, Champ. Fr. Discom. *Pl. 64.* 1874 (*Lachnea trechispora*); Le Gal, Ann. Sci. Nat. XI. **8**: 139. *Fig. 24.* 1947 (*Ciliaria asperior*); Phillips, Brit. Discom. *Pl. 7, Fig. 41.* 1887 (*Lachnea trechispora*); Svrček, Acta Mus. Nat. Pragae **4**(B): *Pl. 6, Figs. 4–7.* 1948 (*Sphaerospora trechispora*).

Specimens examined: New York: *Durand,* on ground, Tichnor's Glen, Canandaigua, July 16, 1902, CUP-D 1500, HOLOTYPE; *Seaver,* on soil, New York Botanical Garden, Aug. 13, 1914, NY; *Batra,* on mossy soil, Cornell Univ., Ithaca, Aug. 13, 1956, WCD 1212.

Finland: *Karsten, ad terram nudam* (no locality), Aug. 24, 1871, H.

Notes: Seaver (**1928**: 43) listed this fungus from North America under the name *Sphaerospora trechispora* (Berk. and Br.) Sacc. and gave *Peziza asperior* Nyl. as a synonym. Several European authors (Boudier **1906**, Le Gal **1947**) have recognized two species of *Scutellinia* with spherical spores, one with relatively large spores, 20–25 μ, and small warts (see FIG. 4B), *Peziza trechispora* Berk. and Br., and another, usually called *Peziza asperior* Nyl. with smaller spores, 14–20 μ, and spine-like warts (see FIG. 4A). It is the latter species which occurs in this country.

The writer has examined both collections mentioned by Nylander in the original description of *Peziza asperior.* The two collections appear to be conspecific. Although both collections have spherical, heavily-warted spores, they lack the well-developed, heavy-walled, rooting hairs typical of the genus *Scutellinia.* The few hairs that are present are thin-walled, hyaline, flexuous, and superficial. The name *Peziza asperior* Nyl. cannot be employed in the sense of Boudier, Le Gal, and others for a species of *Scutellinia.* One of the collections mentioned above must be the type of *Peziza asperior* Nyl., and neither could be considered a *Scutellinia.* Since there does not appear to be another valid name for *Peziza* (*Scutellinia*) *asperior* sensu auct. non sensu Nylander, it seems necessary to describe it as a new species.

SCUTELLINIA TRECHISPORA (Berk. & Br.) Lamb. FIGS. 3B, 4B

Peziza trechispora Berk. & Br., Ann. Nat. Hist. **18**: 77. 1846.

≡ *Lachnea trechispora* (Berk. & Br.) Gillet, Champ. Fr. Discom. 77. 1879.

≡ *Scutellinia trechispora* (Berk. & Br.) Lambotte, Fl. Myc. Belg. Suppl. 299. 1887.

≡ *Sphaerospora trechispora* (Berk. & Br.) Saccardo, Consp. Disc. 4. 1884.

= *Ciliaria trechispora* (Berk. & Br.) Boudier, Nouv. Class Discom. Eur. 105. 1885.

= *Sphaerosporula trechispora* (Berk. & Br.) Kuntze, Rev. Gen Pl. **3**: 530. 1898.

Apothecia moderate-sized, 3–10 mm broad, solitary or scattered; hymenium "Spectrum Red" to "Grenadine Red"; rooting hairs sparse, seldom forked at the base, dark brown, short, 75–250(–300) μ, septate, straight or slightly curved; superficial hairs absent or inconspicuous; asci subcylindrical, 20–25 × 250–300 μ, eight-spored; ascospores spherical, 20–24(–25) μ broad, uniguttulate, sculptured; ascospore sculpturing consisting of rounded warts less than 1 μ high; paraphyses clavate, 1.5–2.5 μ broad below, up to 10 μ broad at the apices.

Habitat: On soil, a European species not known from North America.

Name: From Greek *trecho* = rough and *spora* = seed.

Type locality: Leigh Wood, King's Cliff, England.

Type specimen: in K.

Illustrations: Boudier, Icones Myc. **2**: *Pl. 375.* 1906 (*Ciliaria trechispora*); Cooke, Mycographia *Pl. 33, Fig. 129.* 1876. (*Peziza trechispora*); Lagarde, Ann. Myc. **4**: 208. 1906 (*Lachnea trechispora*); Le Gal, Ann. Sci. Nat. Bot. II. **8**: 111. *Fig. 9B* (*Ciliaria trechispora*); Rehm in Rab. Krypt.-Flora **1**^{3}: 1029. 1894 (*Sphaerospora trechispora*).

Exsiccati: Cooke, Fungi Britannici Exsiccati 288 (*Peziza*).

Specimens examined: Great Britain: *Berkeley* (no substrate, no locality, no date) (CUP-D 6347); *Berkeley,* on soil, Leigh Woods, King's Cliff, Aug. 28, 1845 (K) LECTOTYPE; *Broome* (no substrate) Batheaston Jan. 1867 (CUP-D 4238).

Notes: As noted above, this species is unknown from North America. For a discussion of the relationship of this species to *Peziza asperior* Nyl. see the discussion under *Scutellinia armatospora.*

The original description mentions collections from King's Cliff and Bristol and, somewhat parenthetically, one from Montmorency. The writer has been unable to locate the collection from Bristol. He therefore designates the collection from King's Cliff the LECTOTYPE of *Peziza trechispora* Berkeley.

SCUTELLINIA ASPERRIMA (Seaver) Le Gal[10] FIGS. 1C, 1D, 4C

Melastiza asperrima (Ell. & Ev.) ex Seaver, N. Am. Cup-Fungi (Operculates) 104. 1928.

= *Melastiziella asperrima* (Seaver) Svrček, Acta. Mus. Nat. Pragae **4B**(6): 1948.

[10] The combination was published by Le Gal while this paper was in press.

≡ *Scutellinia asperrima* (Seaver) Le Gal [ut *S. asperrima* (Ell. & Ev.) Le Gal], Bull. Jard. Bot. État. Brux. **29**: 93. 1959.

= *Lachnea barbata* Mass., Jour. Bot. Brit. For. **30**: 161. 1892. (non *Lachnea barbata* (Kunze) Gill. 1879, nec *Ascobolus barbatus* Mass. 1894, nec *Lachnea barbata* Vel. 1934.)

Apothecia up to 1 cm broad, scattered to gregarious, becoming discoid or slightly concave; hymenium bright orange-red, "Spectrum Red" to "Grenadine Red"; rooting hairs scattered, 250–1500(–2000) μ long and as much as 35 μ broad at the base, septate, dark brown, pointed at the apex, straight and unbranched; superficial hairs rare, a few short (150 μ) pale ones visible along the margin; asci 250–300 × 15–20 μ, cylindrical, eight-spored; ascospores 10–13 × 19–23(–25) μ, mode length/width 1.8, long pointed-ellipsoid to sublunulate, hyaline, one- to pluri-guttulate; ascospore sculpturing consisting of a pronounced and regular reticulum, 0.5–1.0 μ high along the sides of the spores, becoming much higher, 1–3(–4) μ, at the poles where it simulates an apiculus; paraphyses clavate, 2–3 μ broad below, 6–7 μ broad above.

Habitat: On rotten wood, throughout the year; type was collected in February.

Name: From Latin, *asperrima* = roughest.

Type locality: Castillo, Nicaragua.

Type specimen: in NY.

Illustrations: Massee, Jour. Bot. Brit. For. **30**: *Pl. 321.* 1892.

Specimens examined: Canal Zone: *M. A. Howe,* on bases of *Elaris melanococca,* Mindi, Jan. 1910 (NY).

Costa Rica: *Dodge and Thomas 4348* (no substrate), Cartago Prov., above Rio Cacao at Pevivale Farm, Sept. 24, 1924 (NY); *Dodge and Catt 5652* (no substrate), Limon Prov., west bank of Rio Pacuare, Oct. 10, 1929 (NY); *Dodge and Goerger 10268* (no substrate), Puntarenas Prov., Flood Plain of Rio Sandalo, Peninsula of Osa, Aug. 27, 1936 (NY).

Cuba: *F. S. Earle 1074,* on rotten banana stalk in sink hole, El Yunque (no date) (NY).

Mexico: *Murrill 928* (no substrate), Motzorongo near Cordoba, Jan. 15, 1910 (NY).

Nicaragua: *C. L. Smith 6,* on bark of dead tree, Castillo, Feb. 1893 (NY, CUP-D), HOLOTYPE.

Surinam: *B. Maguire 24149F* (no substrate), Pinna swamp, Camp No. 3, Jul. 22, 1944 (NY).

Trinidad: *F. J. Seaver 3325,* on wood, Las Lilas, Mar. 24–29, 1921 (NY).

Notes: This species is easily distinguished from all others of the genus by the pronounced and regular reticulum that marks its spores. The spores of other species occasionally show a tendency to form a reticulum by the formation of anastomoses from the bases of originally discrete warts, but the reticulum thus formed is incomplete and irregular and the original warts usually may be distinguished even in mature spores.

Lachnea barbata Massee is a later homonym of *Lachnea barbata* (Kunze) Gillet, an inoperculate discomycete, and is thus unavailable for this taxon. As indicated by Cash (**1953**: 200), Seaver (**1928**: 104) listed "*Lachnea asperrima* Ell. and Ev. in herb.," a ***nomen nudum,*** as a synonym of *Melastiza asperrima* "(Ell. and Ev.)" Seaver. The epithet dates from Seaver's use of it in 1928 where it was accompanied by a description.

Although *Scutellinia asperrima* has not been reported from North America proper, it is so generally distributed in Central America and the Caribbean that it should be sought in Florida and along the Gulf Coast.

Scutellinia pennsylvanica (Seaver) Denison comb. nov. FIG. 4D

Melastiza pennsylvanica Seaver, N. Am. Cup-Fungi (Operculates) 104. 1928.

≡ *Melastiziella pennsylvanica* (Seaver) Svrček, Acta Mus. Nat. Pragae **4B**(6): 61. 1948.

Apothecia large, 5–25 mm broad, scattered, discoid, often with the margin somewhat convoluted; hymenium "Scarlet-Red" to "Grenadine Red," specimens developing under poor light conditions frequently paler to "Light Salmon-Orange"; rooting hairs abundant to scattered, 200–1700(–2300) μ long, septate, straight or slightly curved with a pointed apex; superficial hairs absent or inconspicuous; asci 15–17 × 200–250 μ, cylindrical, eight-spored; ascospores (8–)10–13(–14) × (14–)16–19(–21) μ, mode length/width 1.5–1.6, ellipsoid, strongly sculptured; ascospore sculpturing 0.5–2.0 μ high, consisting of large, 0.5–3.0 μ broad, truncated to somewhat rounded warts that commonly anastomose to form a massive and irregular reticulum; paraphyses subclavate, 3–4 μ broad below, 7–8 μ broad above.

Habitat: On rotting wood, sometimes also on adjacent soil, more rarely on the soil alone; (May–) July to November.

Name: From Pennsylvania, the state in which the type specimen was collected.

Type locality: Youghiogheny River, Pennsylvania.

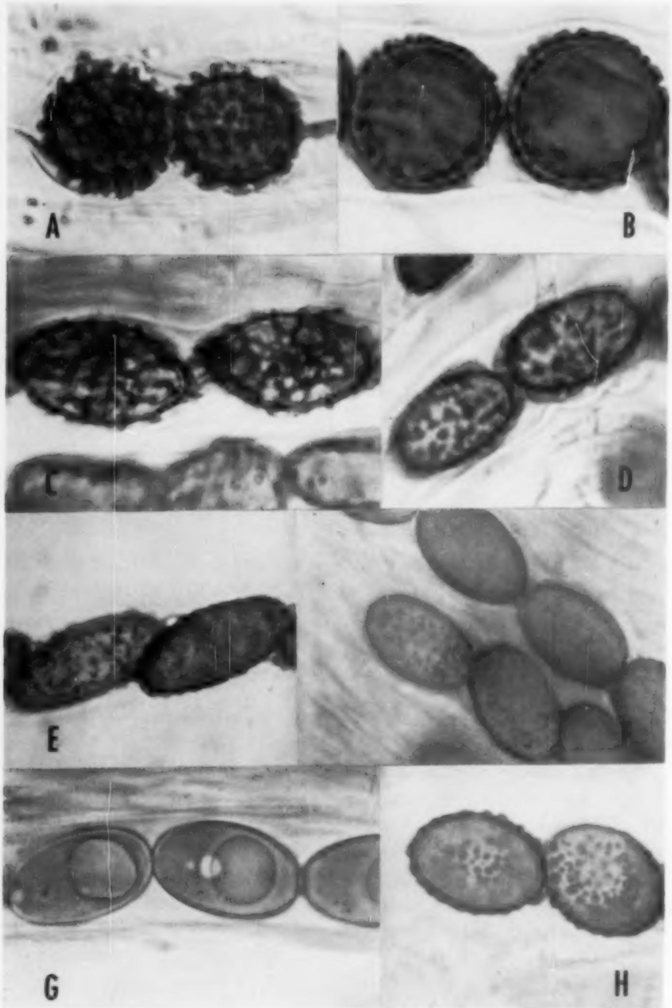

FIG. 4, A–H. Ascospores mounted in cotton blue in lactic acid. All × 1,000. A. *Scutellinia armatospora*, from holotype. B. *Scutellinia trechispora*, from lectotype. C. *Scutellinia asperrima*, from holotype. D. *Scutellinia pennsylvanica*, from holotype. E. *Scutellinia verrucipolaris*, from holotype. F. *Scutellinia scutellata*, from neotype. G. *Scutellinia erinaceus*, from holotype. H. *Scutellinia umbrarum*, from neotype.

Type specimen: in NY.

Specimens examined: Connecticut: *Korf*, on decaying log in woods, Candlewood Lake, Sept. 7, 1946 (*RPK 272*).

Kentucky: *Quinby, Baker, and Bishop*, on burnt log, Iroquois Park, Louisville, Nov. 8, 1933 (NY).

Michigan: *Wehmeyer and Korf*, on old wood, Ann Arbor, 1948 (*RPK 1333*).

New York: *Denison*, on log, west side of Indian Lake, Hamilton Co., Aug. 20, 1954 (*WCD 766*); *Korf*, on rotten stump and ground around stump, Ithaca, Oct. 12, 1944 (*RPK 75*); *Rogerson*, on beech log, Arnot Forest, Schuyler Co., Sept. 15, 1947 (CUP 37138); *Rogerson*, on bark, Six Mile Creek, Ithaca, Oct. 19, 1947 (RPK 773).

Ohio: *C. G. Lloyd* (no substrate), Linwood, May, 1902 (NY); *A. P. Morgan*, on ground (no locality, no date), (NY).

Pennsylvania: *Mrs. G. M. Dallas* (no substrate), Philadelphia (no date), (NY); *W. A. Murrill*, on rotten wood, woods along Youghiogheny River, July, 1905 (NY), HOLOTYPE.

Notes: *Scutellinia pennsylvanica* occupies a position intermediate between *Scutellinia asperrima*, in which the spores are marked with a reticulum reminiscent of the spores of *Aleuria aurantia*, and the species of *Scutellinia* in which the spores are covered with discrete warts. In *Scutellinia pennsylvanica* the spore sculpturing consists of massive warts which are occasionally discrete but which usually run together to form an irregular network. This reticulum never approaches the almost geometrical precision of the sculpturing of spores of *Scutellinia asperrima* nor are the spores apiculate as they are in that species. The individual warts are much higher and cover more of the surface area of the spore than in *S. scutellata* or *S. umbrarum*.

The reticulate nature of the spore sculpturing led Seaver (**1928**: 104) to place this species in the genus *Melastiza*. Svrček (**1948**: 61), however, recognizing the many differences between forms such as *Scutellinia pennsylvanica* with long, bristle-like hairs and the type of the genus *Melastiza*, *M. charteri*, with its poorly developed, adpressed hairs, erected the genus *Melastiziella* for the former group and included both *Melastiza asperrima* and *M. pennsylvanica*. These two species exhibit so many similarities to *Scutellinia scutellata* that they should be included in the genus *Scutellinia*.

Scutellinia verrucipolaris Denison sp. nov. FIG. 4E

Apothecia modica vel minuta, 2–8 mm lata, gregaria, patellaria, thecio rubro; pili radicati numerosi, atrobadii, breves, 100–400(–500)μ longi, acuti, aliquando

pravi; pili superficiales praesertim ad basim numerosi, hyalini, 2–3-septati; asci cylindrici, 240–300 μ longi, octospori; sporae elongato-ellipsoideae, (7.5–)9–11 × (17–)19–22(–24) μ, maturae verrucosae, biguttulatae; verrucis distinctis, teretibus vel subtruncatis, eis ad polos majoribus, 1.0 μ altis, 1.0 μ crassis, eis ad medium minoribus, 0.1–0.5 crassis, 0.1–0.2 altis; paraphyses basi 2–3 μ crassae, apice 6–9 μ angusto-clavatae. Plantae terrestres, aliquando lignicolae, mensibus Julio Augustoque vigentes.

Apothecia medium to small, 2–8 mm broad, gregarious, concave; hymenium "Scarlet" to "Grenadine Red"; rooting hairs moderately abundant, short, 100–400(–500) μ long, septate, dark brown, with pointed apices; a few bent or crooked; superficial hairs present, especially abundant toward the base, hyaline, 2–3 septate; asci cylindrical 240–300 μ long, eight-spored; ascospores (7.5–)9–11 × (17–)19–22 (–24) μ, mode length/width 2.0, sculptured, biguttulate; ascospore sculpturing consisting of discrete, rounded or subtruncate warts reaching a height of 1 μ and an equal breadth, the largest warts most numerous toward the poles, in the equatorial region most of the warts much smaller, 0.15–0.5 μ broad, and barely visible in optical section; paraphyses 2–3 μ broad at base, enlarging to 6–9 μ just below the apex, narrowly clavate to subfusiform.

Habitat: On soil, and occasionally wood, July to August.

Name: From Latin, *verrucosus* = warty, and *polus* = the end of an axis.

Type locality: Allegany State Park, New York.

Type specimen: in CUP.

Specimens examined: New York: *Denison,* on bare soil of stream cut bank, French Creek, Chautauqua Co., Aug. 24, 1953 (*WCD 488*); *Denison,* on bare soil, Bay State Rd., Allegany St. Park, Aug. 27, 1953 (*CUP, WCD 357*), HOLOTYPE; *Denison,* on soil with mosses, Ampersand Mt., Franklin Co., Aug. 23, 1954 (*WCD 834*); *Denison,* on soil with mosses and on wood, Woodland, Ulster Co., July 7, 1954 (*WCD 703*); *Denison,* on soil among mosses, Eaton Lake, Aug. 19, 1954 (*WCD 788*).

Notes: The unusually narrow, biguttulate spores of *Scutellinia verrucipolaris* with their conspicuous warts concentrated toward the poles are sufficient in themselves to distinguish *S. verrucipolaris* from all other species of the genus known to the writer. The fact that *S. verrucipolaris* usually occurs on soil and possesses unusually short hairs furnishes additional aid in identification.

Le Gal (**1954**: 146) has described another narrow-spored, short-haired *Scutellinia, S. stenosperma,* from Europe and Madagascar. The writer has seen the type specimen of this species and what he believes

to be a hitherto unreported collection of the same species from England. Collections of *Scutellinia verrucipolaris* from North America differ from these specimens and from Le Gal's description. The spores of *S. verrucipolaris* range from 17–22 μ in length whereas those of *S. stenosperma* are from 20–27 μ in length. Further, the large warts on the spores of *S. stenosperma* are distributed almost equally over the full length of the spore and are not concentrated toward the poles. Finally, *S. stenosperma* has been reported as occurring on organic debris, old pomace, and rotting bark, whereas all collections but one of *S. verrucipolaris* are restricted to soil. In view of these constant differences it has been decided to treat *Scutellinia verrucipolaris* as a distinct species.

SCUTELLINIA SCUTELLATA (L. ex Fr.) Lambotte FIGS. 1A, 4F

Peziza scutellata L. ex Fr. Syst. Myc. **2**: 85. 1822.

≡ *Humaria scutellata* (L. ex Fr.) Fuckel, Symb. Myc. 321. 1870.

≡ *Lachnea scutellata* (L. ex Fr.) Gillet, Champ. Fr. Discom. 75. 1879.

≡ *Ciliaria scutellata* (L. ex Fr.) Boudier, Bull. Soc. Myc. Fr. **1**: 105. 1885.

≡ *Scutellinia scutellata* (L. ex Fr.) Lambotte, Fl. Myc. Belge Suppl. 299. 1887.

≡ *Humariella scutellata* (L. ex Fr.) Schroeter, Krypt.-Fl. Schles. 3^2: 37. 1893.

≡ *Patella scutellata* (L. ex Fr.) Morgan, Jour. Myc. **8**: 187. 1902.

= *Peziza* (*Sarcoscypha*) *lusatiae* Cooke, Mycographia p. 80. 1876.

≡ *Lachnea lusatiae* (Cooke) Saccardo, Syll. Fung. **8**: 178. 1889.

≡ *Scutellinia lusatiae* (Cooke) Kuntze, Rev. Gen. Pl. **2**: 869. 1891.

≡ *Ciliaria lusatiae* (Cooke) Boudier, Hist. Class. Discom. Eur. 62. 1907.

≡ *Patella lusatiae* (Cooke) Seaver, N. Am. Cup-Fungi 162. 1928.

= *Lachnea balnei* Starbäck, Bih. K. Sv. Vet.-Akad. Handl. **21**: 39. 1895.

Apothecia moderate-sized, 2–12 mm broad, scattered to gregarious, cupulate becoming shallowly concave or discoid; hymenium orange to red, "Spectrum Red" to "Grenadine Red," rarely paler with a pinkish or salmon cast; rooting hairs abundant to scattered (100–)200–700(–1300) μ long, the longest ones concentrated at the margin, 2–12-

septate, dark brown, pointed, straight or slightly curved at the base, not abruptly crooked, simple; superficial hairs usually present; asci 15–20 × 240–320 μ, cylindrical, eight-spored; ascospores (9–)11–14(–17) × (15–)17–19(–23) μ, mode length/width 1.5, moderately sculptured, containing one or more large guttules; ascospore sculpturing small, 0.1–1.0 μ broad, freely anastomosing warts, not visible in optical section; paraphyses subcylindrical to narrowly clavate, 3–5 μ broad below, 5–9 μ broad above, simple or, rarely, branched below.

Habitat: Commonly on rotten wood, bark, or soil; less often on a variety of other substrates: e.g., wood ashes, decaying leaves, and rotting sporophores of *Fomes* spp.; throughout the growing season.

Name: From Latin, *scutella* = a little dish.

Type locality: Torne Lappmark, Jukkasjarvi, Sweden.

Type specimen: in BPI.

Illustrations: Boudier, Ic. Myc. **2**: *Pl. 368.* 1906; Cooke, Mycogr. *Pl. 34, f. 131 & Pl. 37, f. 146 (P. lusatiae).* 1876; Le Gal, Rev. de Myc. **2**: 217. *f. 25C.* 1937; Seaver, N. Am. Cup-Fungi *Pl. 14, f. 2.* 1928; Svrček, Acta Mus. Nat. Pragae **4B**(6): *Pl. 4, f. 1 & 2.* 1924.

Exsiccati: Clements, Cryptogamae Formationum Coloradensium 119 (*Scutellinia*); Fink & Fuson, Ascomycetes of Indiana 620 (*Lachnea*); Krieger, Fungi Saxonici 1270 (*Lachnea hirta*); Lundell and Nannfeldt, Fungi Exsiccati Suecici 1370 (*Lachnea*), NEOTYPE; Rehm, Ascomycetes 1755 (*Lachnea*); Roumeguère, Fungi Gallici Exsiccati 3048 (*Peziza setosa*); Sydow, Mycotheca Marchica 1160 (*Humaria*); Vize, Micro-fungi Britannici 369 (*Peziza*).

Specimens examined (partial list) Alabama: *Denison,* on wood in mud, Cuba, Apr. 2, 1955 (*WCD 952*).

California: *C. R. Orcutt,* on rotten wood, San Diego Co., Sept. 6, 1882 (CUP-D 4317).

Colorado: *F. E. Clements, ad lignum udum muscosumque,* Jack Brook, Aug. 18, 1904, CUP-D.

Indiana: *Fink,* on wood, Franklin Co., May 10, 1918 (CUP-D 10954).

Iowa: *Seaver,* on wood and soil, Iowa City, June 21, 1904 (CUP-D 468).

Louisiana: *A. B. Langlois,* on rotten wood, St. Landry Parish, May 21, 1886 (CUP-D 4322).

Michigan: *Korf,* on mossy log, Cheboygen, June 16, 1948 (*RPK 1264*); *Korf,* on rotten wood, Saginaw Forest, Ann Arbor, July 8, 1948 (*RPK 1315*).

New York: *D. Huttleston,* on rotten log of *Tsuga canadensis,* Casca-

dilla Woods, Ithaca, June 6, 1950 (RPK 2142); *Denison*, on soil, Coy Glen, Ithaca, July 12, 1953 (*WCD 326*); *Denison*, on leaves, Limestone Rd., Allegany St. Park, Aug. 27, 1953 (*WCD 350*); *Denison*, on charcoal, Paradox Lake, June 17, 1954 (*WCD 601*); *W. C. Muenscher*, on moss covered yellow birch, Bergen Swamp, Genesee Co., May 28, 1950 (RPK).

North Carolina: *E. J. Durand*, on rotten wood, Blowing Rock, 1901 (CUP-D 12392).

Oregon: *Carpenter*, on rotten wood (no locality), May 1884 (CUP-D 4320).

Virginia: *W. A. Murrill 452*, on moss covered wood, Mountain Lake, July 1909 (CUP-D 9009).

Canada: *Macoun*, on rotten wood, British Columbia, May 20, 1887 (CUP-D 4318); *Durand*, on rotten wood, Point Albino, Lake Erie, Aug. 1896 (CUP-D 875).

England: *J. E. Vize 369*, (no substrate, no locality, no date) (NY); *Massee* (no substrate), Mulgrave Woods, Whitby, Sept. 1894 (NY).

Germany: *Kritschmar, ad lignum humide jacem*, Sonnewald, July 1845 (K, E), HOLOTYPE of *Peziza lusatiae* Cke.; *W. Krieger* (no substrate), Saxony, June 16, 1897 (CUP-D 4291); *O. S. B. Strasser, auf faulenden Obstresten bei Seitenstetten an Sonntagberg*, Sept. 1907 (CUP-D 11973); *Sydow, an faulendem Holze*, Forst Marrvitz, Landsberg, 1886 (NY).

Scotland: *Fletcher and Korf*, on bark of fallen tree, Glenarbuck Woods, Bowling, Sept. 29, 1950 (*RPK 2148*).

Sweden: *J. A. Nannfeldt 1530, ad lignum et corticem Betulae*, Torne Lappmark, Jukkasjarvi, July 2, 1928 (NY); *Nannfeldt*, on moist soil, overgrown by small mosses, along footpath, Torne Lappmark, Jukkasjarvi, Sweden, 1928 (BPI), NEOTYPE of *Peziza scutellata* L. ex Fr.; *Starbäck* (no substrate, no locality), July, 1894 (CUP-D *4272*), HOLOTYPE of *Lachnea balnei*.

Notes: *Scutellinia scutellata* is by far the most commonly collected species of the genus. In eastern North America it is to be found in nearly every moist bit of woodland from May to September. In the same area an estimated ninety percent of all scutellinias collected from wood belong to this species. There is an appreciable amount of variation from one collection to the next but there is no evident pattern which would permit the ready division of the species into subspecies.

After considerable thought it was decided to designate Lundell and Nannfeldt's Fungi exsiccati Suecici 1369 the NEOTYPE of *Peziza scutellata* L. ex Fr. This selection has the following advantages: 1) it

agrees not only with the original description but also with current usage (vide Le Gal **1937**, Svrček **1948**, Seaver **1928**), 2) it is presumably from the same geographical area as the material on which the original description was based, 3) authentic material is available from a number of established mycological centers. The specimens examined in this study were from the National Fungus Collections at Beltsville, Md. (BPI).

SCUTELLINIA UMBRARUM (Fr.) Lambotte FIG. 4H

Peziza umbrorum [!] Fr., Syst. Myc. **2**: 612. 1823 (as *P. umbrosa*, l.c. p. 85, not *P. umbrosa* Schrad. ex Fr., p. 66).

≡ *Humaria umbrorum* (Fr.) Fuckel, Symb. Myc. 323. 1869.

≡ *Ciliaria umbrorum* (Fr.) Boudier, Bull. Soc. Myc. Fr. **1**: 105. 1885.

≡ *Lachnea umbrorum* (Fr.) Gillet, Champ. Fr. Discom. 209. 1886.

≡ *Scutellinia umbrorum* (Fr.) Lambotte, Fl. Myc. Belge. Suppl. 300. 1887.

≡ *Patella umbrorum* (Fr.) Seaver, N. Am. Cup-Fungi **1**: 161. 1928.

Apothecia medium to large, 8–20 mm broad, scattered to solitary, shallow cup-shaped to discoid or contorted; hymenium orange to red, "Scarlet Red" to "Carmine"; rooting hairs abundant, rather short (75–)150–700(–900)μ long, 2–8-septate, dark brown, pointed; superficial hairs absent or inconspicuous, where present often heavy walled, stout, and very short; asci 15–20 × 240–320 μ, cylindrical, eight-spored; ascospores (12–)14–16(–18) × (19–)20–24(–26)μ, mode length/width 1.4, at maturity with one, less often two, large guttules; ascospore sculpturing consisting of distinct, rounded warts, 0.5–1.5 μ broad and high, scattered over the surface; paraphyses subcylindrical to narrowly clavate, 3.5 μ broad below, 5–9 μ broad above, simple or rarely branched below.

Habitat: On soil or trash, rarely on fragments of rotten wood embedded in moist soil, May to November.

Name: From Latin *umbra* = shade.

Type locality: Nuttallburg, West Virginia.

Type specimen: in CUP.

Illustrations: Boudier, Ic. Myc. **2**: *Pl. 369.* 1906; Cooke, Mycogr. *Pl. 34, f. 138.* 1876; Gillet, Champ. Fr. Discom. *Pl. 68, f. 1.* 1879; Le Gal, Rev. de Myc. **2**: 217. *f. 25E.* 1937; Svrček, Acta Mus. Nat. Pragae **4B**(6): *Pl. 5, f. 3, 4.* 1948.

Exsiccati: Ellis and Everhart, North American Fungi 2nd ser. 2911 (*Peziza*), NEOTYPE; Sydow, Mycotheca Germanica 595 (*Lachnea*).

Specimens examined: California: *Harkness 412* (no substrate, no locality, no date) (CUP-D 4324).

Colorado: *F. Korf and R. P. Korf,* on soil, Big Thompson River, Rocky Mt. Nat'l. Park, Aug. 30, 1948 (*RPK 1450*).

Michigan: *"Wehmeyer, Korf, et al.,"* on soil adjoining swamp, Eber White Woods, Ann Arbor, June 28, 1948 (*RPK 1281*).

New York: *Denison,* on soil and fragments of wood, Mt. Wittenberg, Ulster Co., July 2, 1955 (*WCD 934*); *Denison,* on soil of roadside ditch, Ticonderoga, June 21, 1954 (*WCD 653*); *Denison,* on wet soil, Sprague Rd., Ripley, Aug. 24, 1953 (*WCD 489*); *Denison,* on soil, Town Line Rd., Cherry Creek, Oct. 1, 1953 (*WCD 517*); *Denison and Korf,* on soil in roadside ditch, Labrador Lake, Tully, June 23, 1953 (*WCD 268*).

West Virginia: *L. W. Nuttall,* on a sandbar in the bed of a creek, Nuttalburg, July 1893, Ell. & Ev., N. Am. Fungi 2nd ser. 2911 (CUP), NEOTYPE.

France: *Le Gal, Romagnesi, and Korf,* on the ground in a ditch, Luzarches, Seine-et-Oise, July 27, 1949 (*RPK 1776*); *Le Gal, Romagnesi and Korf,* on ground alongside a stream, Coye-la-Foret, Oise, July 27, 1949 (*RPK 1775*).

Germany: *H. Sydow,* on mossy ground, Brandenburg, June 18, 1906, Sydow Myc. Germ. 595 (CUP).

Notes: This rather common species is known by its broad, strongly marked spores, its short hairs, and its preference for soil as a substrate. It has been recognized by most students of the group (Boudier **1906**: *Pl. 369;* Gillet **1879**: *Pl. 68;* Le Gal **1937**: 217; Seaver **1928**: 161; Svrček **1948**: 58) but there does not appear to be a type specimen. Rehm (**1895**: 1060) not only described this species but also indicated a specimen, Ellis and Everhart's North American Fungi 2911, which agreed with his concept of the species. The writer has examined the material under this label at Cornell University and wishes to designate it the NEOTYPE of *Peziza umbrarum* Fr.

SCUTELLINIA ERINACEUS (Schw.) Kuntze FIGS. 2A, 3D, 4G

Peziza erinaceus Schw., Schr. Nat. Ges. Leipzig **1**: 119. 1822.

≡ *Lachnea erinaceus* (Schw.) Sacc., Syll. Fung. **8**: 182. 1889.

≡ *Scutellinia erinaceus* (Schw.) Kuntze, Rev. Gen. Pl. **2**: 869. 1891.

≡ *Patella erinaceus* (Schw.) Morgan, Jour. Myc. **8**: 188. 1902.

≡ *Trichophaea erinaceus* (Schw.) Le Gal, Prodr. Flor. Myc. Madagascar **4**: 166. 1953, excl. specim., descr., et fig.

= *Patella setosa* sensu Seaver.

Apothecia small, 2–3(–4) mm broad, gregarious, typically with 24 or more apothecia in an area of 4 to 8 square cm, but rarely so crowded as to be distorted by mutual pressure, at maturity discoid to slightly concave; hymenium dull orange with overtones of yellow or brown rather than red, "Zinc Orange" to "Ochraceous-Orange," fading to whitish on drying; rooting hairs abundant, (100–)400–600(–700) μ long and (20–)28(–40) μ broad at the base, inconspicuously septate, dark brown, apex pointed, or rarely quite blunt or with a constriction, many collections having some hairs that are distinctly crooked or that have short prong-like lateral branchlets; superficial hairs lacking or very inconspicuous; asci 270–325 × 12–15 μ, eight-spored, cylindrical; ascospores (9–)11.5(–15) × (14–)17–21(–26) μ, mode length/width 1.7, long ellipsoid, appearing completely smooth in most mounting media, cytoplasmic granules sometimes giving the illusion of very fine markings under an oil-immersion objective; paraphyses clavate or subclavate, 2–5 μ broad at the apices, filled with orange granules when fresh.

Habitat: Well rotted deciduous wood; (July–)August–November (–December).

Name: From Latin, *crinaceus* = a hedgehog.

Type locality: Bethlehem, Pennsylvania.

Type specimen: in Schweinitz Herbarium, PH.

Illustrations: Cooke, Mycographia *Pl. 35, f. 140.* 1877; Bachman, Proc. Ohio Acad. Sci. **5**: *Pl. 1, f. 1–7.* 1909; Svrček, Acta Mus. Nat. Pragae **4B**(6): *Pl. 1, f. 6–7.* 1948.

Excluded illustrations: Le Gal, Prodr. Fl. Myc. Madagascar **4**: *f. 74, 75.*

Exsiccati: Brenckle, Fungi Dakotenses 458 (*Patella setosa*); Ellis and Everhart, North American Fungi 2910 (*Peziza vitellina*); de Thümen, Fungi Austriaci 1013 (*Peziza setosa*); Phillips, Elvellacei Britannici 161 (*Peziza setosa*).

Excluded exsiccati: E. Ule, Appendix Mycothecae Brasiliensis 33.

Specimens examined: Colorado: *F. and R. P. Korf*, on wood, Bear Lake, Rocky Mt. Nat. Pk., Aug. 29, 1948 (*RPK 1442*).

Maine: *F. L. Harvey*, on decaying logs, Orono, Dec. 1887 (CUP-D 2186).

Missouri: *Durand*, very rotten logs, McBaine, Oct. 12, 1912 (CUP-D 9943).

New York: *Durand*, rotten log, McGowan's Woods, Ithaca, Oct. 8, 1902 (CUP-D 1778); *Rogerson*, rotten *Tilia* wood, Cornell Plantations, Ithaca, Sept. 17, 1947 (RPK 701); *French*, on very rotted wood, Scott, N. Y., Sept. 1948 (RPK 1506).

North Carolina: *Durand*, rotten wood, Glen Mary, 1901 (CUP-D 1226).

North Dakota: *Brenckle*, Fungi Dakotensis 458 (NY); *Brenckle 1071*, decaying log in woods, Cheyenne River, Anselm, Aug. 13, 1916 (CUP-D 10480).

Ohio: *Bachman*, on rotten log, Oxford, Nov. 3, 1907 (NY); *G. T. Jones*, on rotten wood, Oberlin, Nov. 1954 (WCD 868).

Pennsylvania: *Schweinitz 788*, on hickory, Bethlehem (no date), (PH-S, NY, CUP-D 3859), HOLOTYPE; *Sumstine*, on wood, Fern Hollow, Allegheny Co., July 23, 1906 (CM).

Vermont: *Burt*, on rotting log, Grand View, Sept. 14, 1897 (CUP-D 1989).

West Virginia: *Ellis and Everhart*, North American Fungi 2910, on rotten wood, Nuttallburg, July 1893 (NY); *Sheldon*, on rotten wood, French Creek, Sept. 12, 1905 (CUP-D 6462); *Leonian and Sleeth*, on wood, Morgantown, Aug. 22, 1933 (NY).

Canada: *Faull*, rotten wood, Algonquin Park, Sept. 25, 1905 (CUP-D 408).

Canal Zone: *Martin 3065*, on wood, Madden Dam, Rio Chagres, July 30, 1935 (NY); *Lichtwardt*, on wood, Barro Colorado, Oct. 1954 (WCD 869).

Nicaragua: *C. L. Smith*, on wood (no locality, no date), (NY).

Notes: Its small size, intensely gregarious habit and yellowish pigmentation make *Scutellinia erinaceus* the easiest species of the genus to recognize in the field. Small specimens of *Scutellinia scutellata*, with which it is most likely to be confused, may usually be distinguished by their deeper red color. In the dried state, long ellipsoid spores without markings, and moderately short, often crooked hairs serve to separate *S. erinaceus* from *S. scutellata* with its broader, sculptured spores and longer hairs.

In the past the fungus, here treated as *Scutellinia erinaceus*, has been recognized by some authors (Phillips **1887**: 406; Seaver **1928**: 166) under the name *Peziza setosa* Nees. However, the name *Peziza setosa* Nees has been used with equal frequency for material that clearly belongs to *Scutellinia scutellata* (Le Gal **1945**). For example, specimens in the Schweinitz Herbarium labeled *Peziza setosa* Nees are *Scutellinia scutellata*. In an effort to determine which use of the name is correct the writer has tried without success to obtain material from Nees's herbarium. It is proposed that until authentic type specimens can be located the name *Peziza setosa* Nees be considered a *nomen dubium*.

In a recent paper Le Gal (**1953**: 166) uses the name *Trichophaea*

erinaceus (Schw.) Le Gal for two collections of discomycetes, one by Ule from Brazil (Appendix Mycothecae Brasiliensis 33) and the other from Madagascar. The writer has seen some of the Brazilian material. Although he could find none of the extremely long hairs (up to 2500 μ) metioned by Mme. Le Gal, the fungus could be distinguished from *S. erinaceus* on other grounds. The spores, for example, were nearly unmarked in the equatorial region but bore distinct markings over both poles. It is suggested that Ule's material, and presumably that from Madagascar, represents a species different from *Scutellinia erinaceus* (Schw.) Kuntze and perhaps is deserving of a new name.

As indicated above, Seaver (**1928**: 166) applied the name *Patella setosa* to this species. Later in the same paper (p. 178) he also included the name *Patella erinaceus*. That he was aware of the similarity between the two is indicated by his note accompanying a slide of authentic material of Schweinitz's type of *P. erinaceus* which reads, "Looks like *L. setosa*. Cannot determine color of disc in dried plants."

EXCLUDED SPECIES AND SYNONYMS

ASCOBOLUS BARBATUS Massee and Crossland

Ascobolus barbatus Massee and Crossland *in* Massee, Grevillea **22**: 99. 1894.

Specimens examined: England: *Massee* (no locality, no substrate, no date), (NY), HOLOTYPE.

Notes: Massee (**1894**: 99, **1895**: 167) describes and figures this fungus as a discomycete with *Scutellinia*-type hairs, a red hymenium, and *Ascobolus*-type spores. A note accompanying the type specimen reads, "A *Lachnea* upon which spores from a neighboring *Ascobolus denudatus* have been shot, B. O. Dodge." The writer has examined the type specimen and confirms Dr. Dodge's observation. The spores contained within the asci are typical of those of a *Scutellinia* but they are immature. It is proposed that this name be rejected on the grounds that its characters were derived from two discordant elements, an immature *Scutellinia* and the spores of an *Ascobolus*, and that neither element would make a satisfactory type (vide Int. Code Bot. Nom. 1956, Art. 66).

LACHNEA BARBATA Massee

Lachnea barbata Massee, Jour. Bot. **30**: 163. 1892 (non *L. barbata* (Kuntze) Gillet 1879, nec *L. barbata* Velenovsky 1934).

Notes: All that could be found of the type of this species was Massee's original watercolor sketch. There is little doubt, however, that

it is the same species as *Scutellinia asperrima.* The name *Lachnea barbata* Massee is a later homonym of *Lachnea barbata* (Kuntze) Gillet. No evidence has been found to indicate that the epithet *barbata* had had been validated by transfer to another genus prior to the time that Seaver (**1928**: 104) validated "*Lachnea asperrima* Ell. and Ev." by publishing a description for it. *Lachnea barbata* Massee is thus a synonym of *Scutellinia asperrima* (Seaver) Denison.

LACHNEA CERVICOLOR Ellis and Everhart

Lachnea cervicolor Ellis and Everhart, Proc. Acad. Nat. Sci. Phila. **1893**: 145. 1893.

Specimens examined: Canada: *Macoun,* on rotten wood (no locality, no date) (CUP-D 4275); HOLOTYPE.

Notes: This species has no rooting hairs and appears to be related to *Humaria hemisphaerica.* It is not a *Scutellinia.*

LACHNEA CHRYSOTRICHA Rehm

Lachnea chrysotricha Rehm, Ann. Myc. **5**: 520. 1907.

Specimens examined: Michigan: *E. T. and S. A. Harper,* on rotten wood, Sailors Encampment, Aug. 1897 (S), HOLOTYPE.

Notes: This is not a *Scutellinia,* certainly not a synonym of *S. erinaceus* as Seaver (**1928**: 178) suggests. The well-developed superficial hairs and large size indicate that it is probably congeneric with *Humaria hemisphaerica.*

LACHNEA SUBCRINITA Rehm

Lachnea subcrinita Rehm, Ann. Myc. **7**: 535. 1909.

Specimens examined: Michigan: *E. T. and S. A. Harper,* on rotten wood, Frankfort, Sept. 1908 (S), HOLOTYPE.

Notes: This is a very interesting species. Its spores with their wrinkled but otherwise unsculptured outer sheaths are reminiscent of the genus *Cheilymenia* and its hairs are within the range of variability for that genus although they are too pale for a *Scutellinia. Lachnea subcrinita* cannot be considered conspecific with *Peziza setosa* Nees in either of the senses in which that name has been employed.

LACHNEA VITELLINA (Pers. ex Fr.) Phillips = *Cheilymenia dalmeniensis* (Cke.) Boudier (see Lundell and Nannfeldt **1946**: 1371).

PEZIZA ASPERIOR Nylander

Peziza asperior Nylander, Not. Sällsk. Fauna Flor. Fenn. Förh. **10**: 21. 1869.

≡ *Leucoloma asperior* (Nyl.) Rehm, Ber. Naturh. Ver. Augsburg **26**: 6. 1881.

≡ *Sphaerospora asperior* (Nyl.) Sacc., Syll. Fung. **8**: 188. 1889.

≡ *Sphaerosporula asperior* (Nyl.) Kuntze, Rev. Gen. Plant. **3**^{3}: 530. 1898.

≡ *Ciliaria asperior* (Nyl.) Boudier, Hist. Class. Discom. Eur. 62. 1907.

≡ *Scutellinia asperior* (Nyl.) Dennis, Kew Bul. **1955**: 571. 1955.

= *Sphaerospora perplexa* Seaver, N. Am. Cup-Fungi 45. 1928.

Specimens examined: New York: *Seaver,* on ground in woods near Yonkers (NY), HOLOTYPE of *Sphaerospora perplexa* Seaver.

Finland: *Brenner,* on soil, Raveniemi, 1863 (H), LECTOTYPE; *Karsten,* on soil, Jalasjarvi, July 1864 (H).

Notes: The two collections from Finland are those mentioned in Nylander's original description of the species. They appear to be identical. The second collection is represented by such a small amount of material that it would make an undesirable type specimen. The writer, therefore, designates the collection from Raveniemi the LECTOTYPE of *Peziza asperior* Nylander.

This name cannot be used for a *Scutellinia.* The only hairs found on the type specimen were a very few hyaline, thin-walled, flexuous ones arising from the exterior of the excipulum. The globose cells of the excipulum, the spherical, sculptured spores, the red to yellow hymenium, and the substrate all indicate the probability that *Peziza asperior* Nylander belongs in the genus *Lamprospora.*

PEZIZA LAETICOLOR Karsten

Peziza laeticolor Karsten, Symb. Myc. Fenn. **1**: 66. 1871.

≡ *Scutellinia laeticolor* (Karst.) Kuntze, Rev. Gen. Plant. **2**: 869. 1891.

Specimens examined: Finland: *Karsten* (no substrate, no locality, no date), (NY), AUTHENTIC (possibly holotype).

Notes: Assuming that the specimen examined was the type specimen, or at least authentic, *Peziza laeticolor* is not a synonym of *Scutellinia scutellata* as suggested by Seaver (**1928**: 159). The apothecial hairs of this specimen are superficial in origin. Probably *Peziza laeticolor* Karsten belongs in or near the genus *Trichophaea.*

PEZIZA SEQUOIAE Phillips

Peziza sequoiae Phillips, Grevillea **7**: 22. 1878.

≡ *Lachnea sequoiae* (Phill.) Sacc., Syll. Fung. **8**: 176. 1889.

≡ *Scutellinia sequoiae* (Phill.) Kuntze, Rev. Gen. Plant. **2**: 869. 1891.

≡ *Patella sequoiae* (Phill.) Seaver, N. Am. Cup-Fungi **1**: 167. 1928.

Specimens examined: California: *Harkness 638*, on bark and decaying foliage of *Sequoia gigantea* (no locality, no date), (K), HOLOTYPE.

Notes: The apothecial hairs in this species are superficial in origin and too flexuous for a species of *Scutellinia*. The spores appear smooth in most mounting fluids but exhibit faint markings when stained with cotton blue. These markings are of a type unknown to the writer from any other species of discomycete.

SCUTELLINIA COPRINARIA (Cooke) Kuntze ≡ *Cheilymenia coprinaria* (Cooke) Boudier.

SCUTELLINIA DALMENIENSIS (Cooke) Kuntze ≡ *Cheilymenia dalmeniensis* (Cooke) Boudier.

SCUTELLINIA GILVA (Boud.) Boudier ≡ *Tricharia gilva* (Boud.) Boudier.

SCUTELLINIA MELALOMA (Alb. and Schw. ex Pers.) Kuntze ≡ *Anthracobia melaloma* (Alb. and Schw. ex Pers.) Boudier.

SCUTELLINIA PULCHERRIMA (Crouan) Kuntze ≡ *Cheilymenia pulcherrima* (Crouan) Boudier.

SCUTELLINIA SCUBALONTA (Cke. and Gerard) Kuntze ≡ *Cheilymenia scubalonta* (Cke. and Gerard) Boudier.

SCUTELLINIA STERCOREA (Pers. ex Fr.) Kuntze ≡ *Cheilymenia stercorea* (Pers. ex Fr.) Boudier.

SCUTELLINIA THELEBOLOIDES (Alb. and Schw. ex Fr.) Kuntze ≡ *Cheilymenia theleboloides* (Alb. and Schw. ex Fr.) Boudier.

SCUTELLINIA VITELLINA (Pers. ex Fr.) Kuntze = *Cheilymenia dalmeniensis* (Cke.) Boudier (see Lundell & Nannfeldt **1946**: 1371).

SEPULTARIA RUBROPURPUREA Clements

Sepultaria rubropurpurea Clements, Bot. Surv. Nebr. **4**: 15. 1896.
= *Lachnea rubropurpurea* (Clements) Sacc. and Syd. in Sacc., Syll. Fung. **14**: 755. 1899.

Specimens examined: Nebraska: *Clements,* on sandy bank, Hazel Creek Canyons, Brown Co. (no date), (NY), HOLOTYPE.

Notes: This is not a *Scutellinia;* thus it cannot be a synonym of *Scutellinia umbrorum,* as Seaver (**1928**: 161) suggests. The apothecial hairs arise in fascicles from superficial, dark-walled cells. It is most probably related to *Humaria hemisphaerica.*

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LITERATURE CITED

Boudier, E. 1885. Nouvelle classification naturelle des Discomycètes charnus connus généralement sous le nom de Pézizes. Bull. Soc. Myc. Fr. **1**: 91–120.

——. 1905–1910. Icones Mycologicae ou Iconographie des Champignons de France. Paris.

Cash, Edith K. 1953. A record of the fungi named by J. B. Ellis, Part 2 (issued by the Division of Mycology, U. S. Dept. Agr., Beltsville).

Cooke, M. C. 1875–1879. Mycographia, seu Icones Fungorum **1**: Discomycetes. London.

Corner, E. J. H. 1929. Studies in the morphology of Discomycetes. II. The structure and development of the ascocarp. Brit. Myc. Soc. Trans. **14**: 275–291.

Durand, E. J. 1900. The classification of the fleshy Pezizineae with reference to the structural characters illustrating the bases of their division into families. Bull. Torrey Bot. Club **27**: 463–494.

Fuckel, K. W. G. L. 1870. Symbolae mycologicae. Jahrb. Nassauischen Ver. Naturk. **23–24**.

Gillet, C. C. 1879. Champignons de France; les Discomycètes. Alençon.

Gwynne-Vaughan, Helen C. I., and H. S. Williamson. 1933. The asci of *Lachnea scutellata.* Ann. Bot. **47**: 375–383.

Heim, Panca. 1947. Études sur la localization des pigments carotiniens ches les champignons. Rev. de Myc. **12**: 104–126.

Kanouse, Bessie. 1958. Some species of the genus *Trichophaea.* Mycologia **50**: 121–140.

Korf, R. P. 1952. Two techniques for showing spore markings in operculate discomycetes. Brit. Myc. Soc. Trans. **35**: 24–25.

Kuntze, C. E. O. 1898. Revisio generum plantarum. Pars III. Leipzig.

Lagarde, J. 1908. Contribution à l'étude des Discomycètes charnus. Ann. Myc. **5**: 125–256.

Lambotte, E. 1887. Flore mycologique de Belge. Supplement 1. Brussels.

Lanjouw, J., and F. A. Stafleu. 1956. The herbaria of the world. Regnum Veg. **6**.

Le Gal, Marcelle. 1937. Florule mycologique des Bois de la Grange et de l'Étoile. Rev. de Myc. **2**: 200–224.

——. 1945. Contributions à l'étude des *Ciliaria*. 1. Un *Ciliaria* peu connu: *C. lusatiae* (Cooke) Boud. Bull. Soc. Myc. Fr. **61**: 47–51.

——. 1947. Recherches sur les ornementations sporales des Discomycètes operculés. Ann. Sci. Nat. Bot. XI. **8**: 73–297.

——. 1953. Les Discomycètes de Madagascar. Prodr. Fl. Myc. Madagascar **4**. Paris.

Lundell, S., and J. A. Nannfeldt. 1934–. Fungi exsiccati Suecici. Upsala.

Maire, R. 1937. Fungi Catalaunici II. Treb. Mus. Ciències Nat. Barcelona.

Massee, G. 1894. New or critical British fungi. Grevillea **22**: 97–99.

——. 1895. British fungus-flora **4**. London.

——. 1897. A monograph of the Geoglossaceae. Ann. Bot. **11**: 225–306.

Morgan, A. P. 1902. The discomycetes of the Miami Valley, Ohio. Jour. Myc. **8**: 179–192.

Phillips, W. 1887. A Manual of the British Discomycetes. London.

Rehm, H. 1886–1896. Ascomyceten: Hysteriaceen und Discomyceten. Rab. Krypt.-fl. Deutschl. Oesterr. Schw. 2 Aufl. **1**: III Abt. Leipzig.

Ridgway, R. 1912. Color standards and color nomenclature. Washington.

Saccardo, P. A. 1889. Sylloge fungorum omnium hucusque cognitorum. **8**. Pavia.

Seaver, F. J. 1928. The North American cup-fungi (operculates). New York.

Svrček, M. 1948. Česke druhy podceledi Lachneoideae (cel. Pezizaceae). Acta Mus. Nat. Pragae **4B**[6]: 1–95.

A NEW HALOPHILIC SPECIES OF EUROTIUM [1]

C. M. Christensen,[2] G. C. Papavizas,[3] and C. R. Benjamin [4]

(with 6 figures)

In 1954, samples of wheat obtained from terminal elevators in several parts of the country were stored in 4 oz prescription bottles with screw caps having rubber liners. The wheats had moisture contents between 13 and 14 per cent, wet weight basis, when placed in the bottles. After about 2 years, mycelium was observed on the embryo surface of many of the seeds. A number of seeds of each of several samples were placed, without prior surface disinfection, on malt agar containing 15 per cent sodium chloride, a medium we frequently have used to isolate *Aspergillus restrictus* from seeds. After 10 days, the surface of the germs of most seeds was covered with white perithecia. The perithecia developed on the germs of hard red winter wheat from Omaha, Nebraska, soft red winter wheat from Marietta, Pennsylvania, and Chicago, Illinois, and white wheat from Buffalo, New York, and Maumee, Ohio. Several isolates of the fungus were studied in some detail and the fungus appears sufficiently different from known species of *Eurotium* and *Aspergillus* to warrant description as a new species.

Eurotium halophilicum sp. nov. Figs. 4–6.

Peritheciis minutis, globosis vel subglobosis, superficialibus, sine ostiolo, albis vel dilute flaveolis, (125–)150–180(–240) μ diam., pariete fragili; ascis globosis vel subglobosis, octosporis, cito diffluentibus, 9–14 μ diam.; ascosporis lenticularibus, hyalinis, cristis aequatorialibus duobus humilibus ornatis, superficiebus aequatorialibus echinulatis, 5.5–7.5(–9) × 4–5(–7) μ; conidiophoris 300–500(–750) μ longis, 6–10 μ diam., hyalinis vel dilute viridibus, plerumque levibus, membranis 0.5–0.7 μ diam.; vesiculis globosis, subglobosis vel lageniformibus, per quartas tres superiores fertilibus; sterigmatibus uniseriatis, interdum etiam in tumoribus subvesicularibus

[1] Paper No. 4088, Scientific Journal Series, etc.

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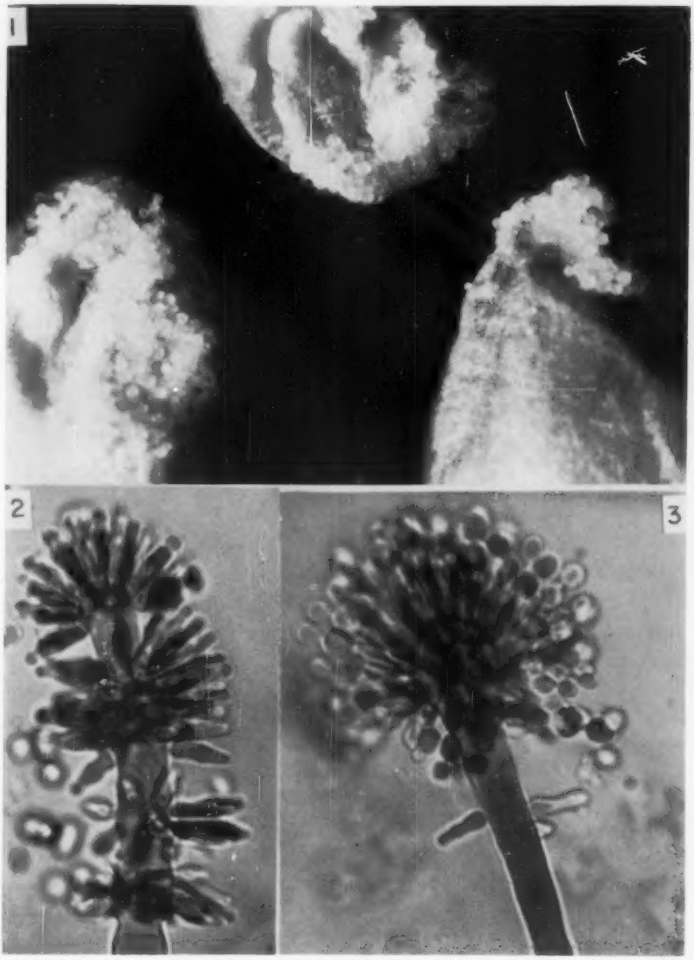

FIG. 1. Masses of white perithecia of *Eurotium halophilicum* developing on embryo of wheat seeds cultured on malt agar containing 15 per cent sodium chloride. FIG. 2. An abnormal sporophore of *A. halophilicus*, with sterigmata growing from enlarged portions below the terminal head. FIG. 3. More normal head of *A. halophilicus*, although 2 sterigmata are growing from the stalk below the head. 2 and 3 from cultures on Czapek's agar containing 55 per cent sucrose.

productis; conidiis catenulatis, hyalinis vel dilute cyaneoviridibus, globosis, ellipticis, pyriformibus vel irregularibus, continuis, echinulatis, 6.0–11.0(–15) × 4.0–6.5(–8) μ; statibus ambobus halophilis.

Status conidicus est **Aspergillus halophilicus** sp. nov.

Hab.: In culturis e *Tritico aestivo* L. Amer. bor.

Etym. ἁλός (salt) + φιλῐκός (characterized by loving).

TYPE: NRRL 2739, dried specimens of which will be deposited in the herbaria of the National Fungus Collections (Plant Industry Station, Beltsville, Maryland), the New York Botanical Garden (New York, N. Y.) and the Commonwealth Mycological Institute (Kew, Surrey, England).

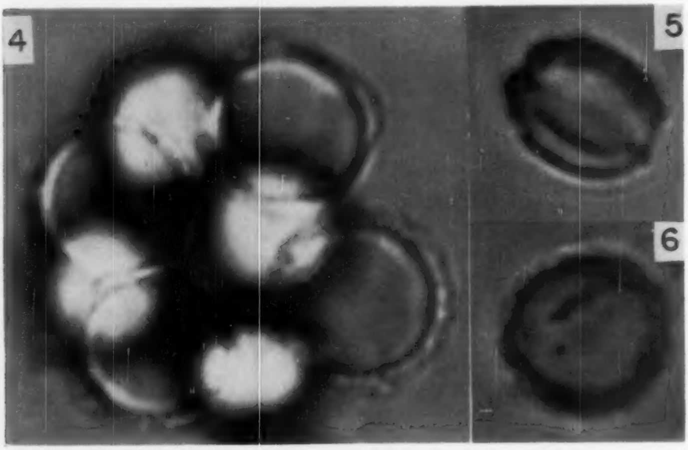

FIG. 4. Ascus of *E. halophilicum*. FIGS. 5 and 6. Ascospores in side and face view.

The salient characteristics of the fungus are as follows. Conidial stage (described from colonies on PDA + 20 per cent sodium chloride, incubated 45 days at room temperature): heads Pea Green to Sage Green (Ridgway, plate XLVII), arising from white, appressed mycelium; spore mass globose when young, loosely radiate when mature, mostly 70–130 μ, occasionally 175 μ in diam.; conidiophores 300–550 μ, occasionally 750 μ long, 6–10 μ in diam., hyaline or light green, smooth or with faint wavy markings, wall 0.5–0.7 μ thick; vesicle globose to subglobose or club-shaped, occasionally with one or two enlargements below the main or terminal vesicle; sterigmata in one series, 3–6 μ wide, 6–14 μ long, covering only a portion of the top or the upper half or three-fourths of the vesicle, sometimes growing from the swellings below the terminal vesicle (FIGS. 2, 3); conidia globose, elliptical, pyriform,

or irregular, spiny, hyaline to light blue-green, mostly 4.0–6.5 × 6.0–11.0 μ, a few up to 8 × 15 μ.

The perfect stage (from colonies on Czapek's agar containing approximately 70 per cent sucrose, incubated 45 days at 25°) as follows: perithecia white to Maize Yellow, becoming Buff Yellow with age (Ridgway, plate IV), spherical to subspherical or irregular, mostly 150–180 μ, but in some cases 125–240 μ in diam.; asci 9–14 μ in diam., spherical or nearly so; ascospores hyaline or very light green, lenticular, with equatorial surface rough, with furrow shallow and bordered by low ridges, mostly 4–5 × 5.5–7.5 μ, but occasionally 7 × 9 μ in size.

TABLE 1

COLONY DIAMETER, COLOR OF MYCELIUM, AND SPORULATION OF EUROTIUM HALOPHILICUM ON VARIOUS AGAR MEDIA, AT 25° C

Basic medium	% NaCl	Colony diam. in mm after 45 days	Colony color	Spores produced
Malt agar	0	0		
	5	0		
	10	Trace		
	15	40		
	20	41	White to pale yellow; reverse pale buff-yellow	Conidia moderately abundant
PDA	5	0		
	10	0		
	15	46		
	20	34	White to pale yellow; reverse buff-yellow to apricot yellow	Conidia abundant; perithecial initials moderately abundant
	% sucrose			
Czapek's	35	0		
	45	0		
	55	32		
	70	40	White to pale yellow; reverse buff-yellow	Conidia few or none; perithecia abundant

Cultures on agar media: colony characters on various agar media are summarized in TABLE 1. The fungus has been inoculated repeatedly onto a number of different media, has consistently failed to grow on media containing less than about 10 per cent sodium chloride or 40 per cent sucrose, and has consistently grown more rapidly on the higher concentrations of salt or sugar. Spores have germinated and mycelium has grown on malt agar saturated with sodium chloride (with salt crystals present in the agar) and on Czapek's agar saturated with sucrose.

The fungus was inoculated onto wheat seeds having a moisture content of 13.0–13.5 per cent, wet weight basis, and the seeds stored

in tightly stoppered bottles in the laboratory. Very little mycelium developed on these seeds. After being stored for 1 year, seeds were removed and placed on malt agar containing 15 per cent sodium chloride, and perithecia of *E. halophilicum* formed abundantly on and adjacent to the germ, as shown in FIG. 1.

DISCUSSION

Eurotium halophilicum is clearly related to the other members of the genus by the morphology of both its ascocarpic and conidial states. It resembles the other species in its type of ascocarpic initials, its pseudoparenchymatous cleistothecial wall, its asci which apparently result from crozier formation, and its ascospore shape and ornamentation. Also like other species, its conidial apparatus is of the *Aspergillus* type. It differs from other species in that its cleistothecial wall and sterile mycelium lack the bright yellow and orange pigments generally considered characteristic, its ascospore size is intermediate to the so-called "small-spored" and "large-spored" groups, it requires very high concentrations of sugar or salt for growth, and its conidial state, *Aspergillus halophilicus*, is more nearly typical of the *A. restrictus* series of Thom and Raper (**2**) than of any other series even though none of the members of this series has heretofore been reported with a perfect stage and none of the approximately 30 different isolates that we have cultured from grain and other materials has ever produced perithecia. Certainly in its adaptation to a high osmotic pressure, both in its natural habitat and in culture, *E. halophilicum* closely resembles some of the members of the *A. restrictus* series.

Regarding its occurrence, we do not at present know whether the fungus is of relatively rare occurrence and limited distribution, or whether it is common in certain habitats but merely difficult to isolate.

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LITERATURE CITED

1. **Ridgway, R.** Color Standards and Color Nomenclature. 43 pp. Illustrated. Washington, D. C. 1912.
2. **Thom, C., and K. B. Raper.** A Manual of the Aspergilli. 373 pp. Williams and Wilkins, Baltimore, Md. 1945.

ISOLATION OF A NEW SPECIES OF ALEURISMA FROM SOIL IN AUSTRALIA AND NEW GUINEA

D. Frey [1]

(WITH 4 FIGURES)

In previous papers (**3**, **4**, **6**) the use of human hair for isolating keratinophilic fungi from soil has been reported and a new species, *Trichophyton terrestre* described. The present paper deals with another new species isolated on human hair from soil samples collected in New Guinea and New South Wales.

Aleurisma keratinophilum sp. nov.

Fungus terrestris, mycelio septato, ramoso, hyalino; conidiis (aleuriosporis) obovoideis, hyalinis, solitariis, acrogenis vel lateralibus, aseptatis ($12.9 \times 14.5\ \mu$), parietibus crassis (0.5–$1.0\ \mu$) et levibus cum conidiophoris continuis, ad apicem obtusis et ad basim truncatis. Habitat in humo Australiensi et Novo-Guineensi. Noxius cavibus.

Cultura in agaro Sabouraudi alba, lanosa, in margine abrupta, sulcos circam umbonem praebita, quae post dies multas in conspectum pulvereum et sulfureum convertit.

The fungus was isolated from nine soil samples, of which five were collected in New South Wales, four near Sydney, one at Murrurundi, and four in New Guinea, two of these last from Goroka Valley and two from Kavieng.

Hairs on a soil plate after 8–12 weeks were covered with white fluffy mycelium. Microscopic examination showed septate mycelium with numerous obovoid, smooth and thick-walled, hyaline conidia. Later the hairs became fragmented and finally disappeared completely.

Appearance of Colony

On Sabouraud-cycloheximide-neomycin agar the moderately quickly growing colonies (70 mm in diameter, 21 days) were white and fluffy with concentric furrows, a central umbo and a rather abrupt margin.

[1] Working with the aid of a full-time grant from the National Health and Medical Research Council of Australia.

The reverse of the colony was brownish-yellow. With age the colonies became cream-coloured and powdery (FIG. 1).

Microscopic Appearance

Preparations were made by using the cellophane technique of Fleming and Smith (**5**).

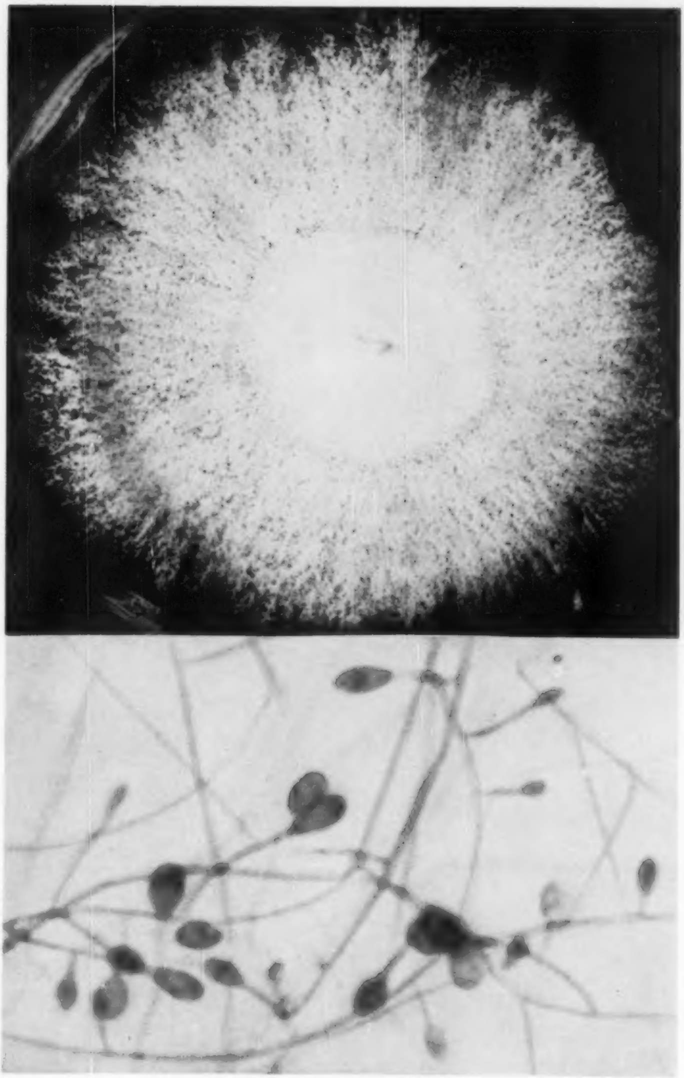
The mycelium is branched, septate and hyaline. The conidia (aleuriospores) are hyaline, obovoid, solitary, terminal or lateral, nonseptate ($12.9–14.5 \times 6.4–8.0\,\mu$), smooth and moderately thick-walled ($0.5–1.0\,\mu$), rounded at the apex and flattened at the base. As the wall of the conidium is in direct continuity with that of the supporting hypha, the conidia are non-deciduous, and are liberated only when an irregular break occurs in the hyphal wall, bearing with them a frill at their base, the remnant of the wall proximal to the conidium from the point of rupture. Other conidia are produced in a position lateral to, and sessile upon, the aerial hyphae (FIG. 2).

This fungus is therefore characterized by the production of aseptate, obovoid conidia. It would appear to have been isolated previously by White et al. (**7**) during a study of the degradation of woollen fabrics. However, they did not name it, merely referring to it as a "*Ctenomyces*-like fungus" on the suggestion of C. W. Emmons.

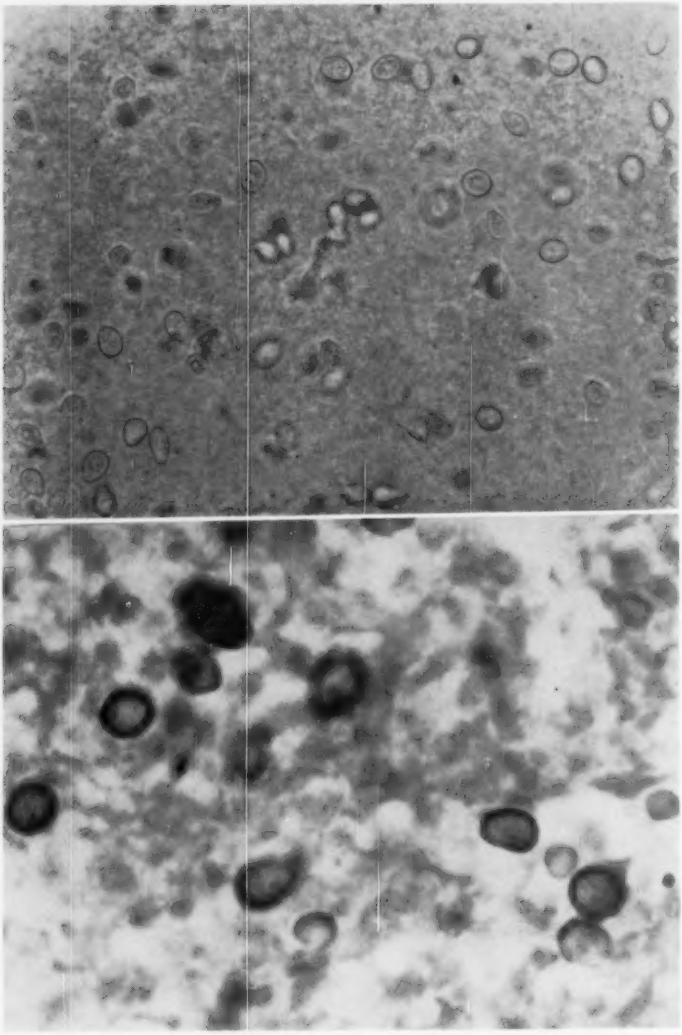
The genera *Trichophyton, Microsporum, Aleurisma* and certain genera within the Gymnoascaceae all produce aseptate conidia. However, the present fungus cannot be referred to *Trichophyton* or *Microsporum* (for it lacks septate macroconidia), nor to the gymnoascaceous genera (for no sexual stage has been produced). In conidial characteristics, it closely resembles *Aleurisma* Link ex. Fr. as used by Bisby (**1**) in his transfer of *Sporotrichum carnis* Brooks and Hansford (**2**) to *Aleurisma.* The conidia of the present fungus are certainly far larger than those of *Aleurisma carnis* but it seems preferable to place it in *Aleurisma* as a temporary measure rather than to create a new genus.

Pathogenicity Tests

The inoculum was prepared from four- to five-weeks-old colonies grown on Sabouraud-cycloheximide-neomycin agar by adding 6 ml of sterile normal saline to the slant and by gentle scraping of the surface growth. Into each of seven guinea pigs 0.1 ml of this saline suspension was injected intradermally in the right side of the abdomen, and 0.4 ml of the same suspension was given subcutaneously into the left side of



FIGS. 1, 2. *Aleurisma keratinophilum*. FIG. 1 (above). Sabouraud's glucose agar with cycloheximide and neomycin, 21 days. FIG. 2 (below). Slide culture on the same medium, showing conidia, 10 days. × 400.



FIGS. 3, 4. *Aleurisma keratinophilum.* FIG. 3. Direct mount of pus in 10% KOH from subcutaneous abscess of guinea pig showing round to obovoid thick-walled spores. × 400. FIG. 4. Section of skin, showing round to obovoid thick-walled spores in the subcutaneous layer. Periodic acid-Schiff stain. × 800.

the abdomen. All the guinea pigs showed the same reaction pattern, which can be illustrated by the following example:

Two weeks after inoculation the right side of the abdomen showed a patch of erythema about 2.5 cm in diameter and some scaling of the skin at the site of the intradermal inoculation. On the left side, after 5 to 10 days, a firm swelling, 6×12 mm in diameter, developed at the site of the subcutaneous injection. Pus was found on puncture. The skin scraping and the content of the nodule were examined microscopically in 10% potassium hydroxide, and were also subcultured on Sabouraud agar containing cycloheximide and neomycin. Microscopic examination of the pus showed round (av. $11.2\,\mu$ in diameter) to obovoid, thick, smooth-walled spores with granular cytoplasm ($14.5–16.1 \times 8.0–14.5\,\mu$) (FIG. 3); that of the skin scraping showed some small round spores.

Pure cultures of the fungus were recovered from the skin scrapings and from the pus 8 to 10 days after inoculation on Sabouraud-cycloheximide-neomycin agar.

Three weeks after inoculation the subcutaneous nodule began to shrink and a few days later there was no pus on puncture. In four weeks the nodule had disappeared. The surrounding skin showed slight scaling.

One animal was killed 5 days after inoculation. Cultures from liver, spleen, lung and kidney yielded no growth of fungus. Histological preparations of the nodule produced by subcutaneous inoculation showed fungus spores in an abscess in the deep part of the subcutaneous layer. The inflammation extended into the muscular layer but the fungus had not invaded this layer (FIG. 4).

SUMMARY

Aleurisma keratinophilum sp. nov. is a keratinophilic and keratinolytic fungus, which was isolated from nine soil samples collected in New South Wales and New Guinea. It grows readily on hair and on Sabouraud-cycloheximide-neomycin agar. Structurally, it is characterized by large, aseptate obovoid conidia. Lesions were produced in guinea pigs by intradermal and subcutaneous inoculation.

ACKNOWLEDGMENTS

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Sydney, for the examination of histopathological specimens; to Dr. E. B. Durie of the Royal North Shore Hospital, Sydney, for help and advice, to Miss M. Simpson for making the photographs shown in this paper, and to Dr. C. W. Emmons of the National Institutes of Health, Bethesda, Maryland, for help and criticism in the preparation of this paper.

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LITERATURE CITED

1. **Bisby, G. R.** Notes on British Hyphomycetes. Brit. Myc. Soc. Trans. **27**: 101–112. 1944.
2. **Brooks, F. T., and C. C. Hansford.** Mould growths upon cold-store meat. Brit. Myc. Soc. Trans. **8**: 113–142. 1923.
3. **Durie, E. B., and D. Frey.** The isolation of *Microsporum gypseum* from Australian soil. Nature **176**: 936. 1955.
4. **Durie, E. B., and D. Frey.** A new species of Trichophyton from New South Wales. Mycologia **49**: 401–411. 1957.
5. **Fleming, A., and G. Smith.** Some methods for the study of moulds. Brit. Myc. Soc. Trans. **27**: 13–19. 1944.
6. **Frey, D., and E. B. Durie.** The isolation of keratinophilic fungi, including *Microsporum gypseum*, from Australian soil. Australian Jour. Exper. Biol. Med. Sci. **34**: 199–204. 1956.
7. **White, W. Lawrence, G. R. Mandels, and R. G. H. Siu.** Fungi in relation to the degradation of woolen fabrics. Mycologia **42**: 199–223. 1950.

OXYGEN-UPTAKE STUDIES ON GLUCOSE-GROWN AND FATTY-ACID-EXPOSED FUNGUS CELLS [1]

G. T. Johnson and G. J. Dixon [2]

(with 3 figures)

The chain length of saturated fatty acids has been associated with their effect on the growth and respiration of *Spicaria violacea*. The C_2–C_7 and C_{16}–C_{18} acids stimulate, and C_8–C_{14} acids inhibit, O_2 uptake by this organism (Johnson, **1957**). With the exception of myristate (C_{14}), the acids which stimulate O_2 uptake are those which provide for growth (Johnson, **1958**), and those which inhibit O_2 uptake are those which provide unsatisfactory substrates for the mold.

Studies to date (Stokoe, **1928**; Thaler et al., **1939**; Mukherjee, **1952**; Melnick et al., **1954**) tend to indicate that a β-oxidation pathway is involved in fatty-acid degradation by molds. This mechanism, originally proposed by Knoop (**1905**), considered that fatty-acid oxidation proceeds through the formation of a β-keto acid, which is then oxidized at the carbonyl group to the acid with two carbon atoms less, the two-carbon fragment usually being identified with acetic acid. Hence, the metabolism of stearic acid (C_{18}) would proceed to a C_{16} (palmitic acid) intermediate, then through successive stages to C_{14}, C_{12}, C_{10}, C_8, C_6, etc.

If the enzymes involved were adaptive enzymes, data testing the occurrence of the suggested pathway could be obtained using the technique of simultaneous adaptation developed by Stanier (**1947**), as Silliker and Rittenberg (**1951**) have previously done with certain bacterial forms. The present paper reports an investigation initiated along these lines. The data obtained indicate that constitutive rather than adaptive enzymes are involved in fatty-acid oxidation by *Spicaria violacea* cells. The data further suggest that the C_9–C_{13} substrates are not metabolized, either (1) because the enzymes that can do so require different conditions for activity than those that oxidize similar sub-

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strates with different carbon-chain lengths, or (2) because no enzymes, constitutive or adaptive, are present to activate these fatty acids to the acyl CoA form.

MATERIALS AND METHODS

Cells of *Spicaria violacea* were grown for 48 hrs at 25 ± 1° C on a Brunswick rotary-type shaker in a Czapek-Dox mineral-salts solution with 5% glucose as a carbon source. Cells were harvested by centrifugation under sterile conditions, and thrice washed with distilled water. After transfer to a flask containing sterile water and a return to the

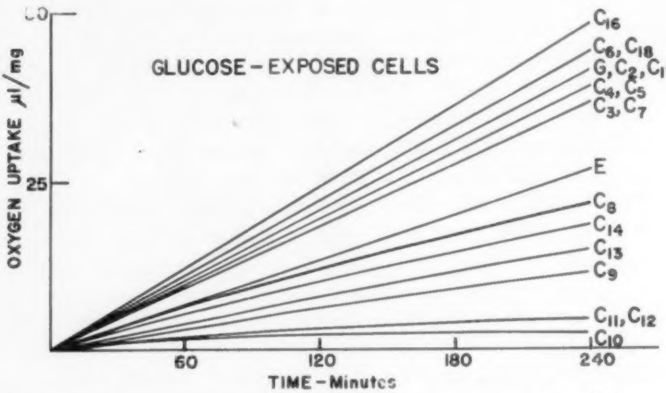

FIG. 1. Oxidation of fatty acids by glucose-exposed cells of *S. violacea*. Cup contents and conditions as indicated in the text. C_{16}, C_{17}, C_{18}, etc., refer to the fatty acid of the chain-length cited. E = endogenous uptake (without substrate). G = glucose.

shaker for 48 hrs more, the cells were again collected by centrifugation, thrice washed with aseptic techniques, and placed in a sterile Czapek-Dox mineral-salts solution containing a 1% concentration of the substrate to which possible adaptation might be made. After 24 hrs in submerged culture on this substrate cells were harvested, thrice washed as before, and the sediment taken up in distilled water to form a suitable cell suspension.

O_2 uptake studies were next made on saturated-fatty-acid substrates of chain lengths from C_2 to C_{18} (except C_{15}, which was not available) and on glucose controls, using standard manometric techniques. All fatty acids (commercial preparations from Fisher, Eastman, and Nutritional Biochemicals) were converted to the potassium soap with potas-

sium hydroxide in absolute alcohol, precipitated and washed with anhydrous ether, and dried in a vacuum desiccator. Each Warburg vessel contained 0.7 ml 0.2 M phosphate buffer, pH 7.2, and 1.0 ml 0.1 M substrate (fatty acids as the potassium soap). The side arm contained 1.0 ml cell suspension and the center well 0.3 ml 6N NaOH. Cups were oxygenated for 3 minutes and equilibrated for 10 minutes before the

TABLE 1

OXYGEN UPTAKE BY SUBSTRATE-EXPOSED CELLS OF SPICARIA VIOLACEA

New substrate	Substrate to which cells exposed							
	Glucose	C_{18}	C_{16}	C_{12}	C_{10}	C_7	C_6	C_5
C_2	++	+	++	±	±	++	++	++
C_3	++	++	+++	±	±	±	±	++
C_4	++	++	+++	±	±	+	+	++
C_5	++	++++	+++++	−	−	+	++	+++
C_6	+++	++++	+++++	−	−	++	++++	+++++
C_7	++	+	++++	−	−	±	++++	+++++
C_8	−	−	++	−	−	−	−	+++
C_9	−	−	−	−	−	−	−	−
C_{10}	−	−	−	−	−	−	−	−
C_{11}	−	−	−	−	−	−	−	−
C_{12}	−	−	−	±	−	−	−	−
C_{13}	−	−	−	−	−	−	−	−
C_{14}	−	−	−	−	−	−	±	−
C_{16}	++++	++++	+++++	++	++	++++	++++	++++
C_{17}	++	++++	+++	−	−	+++	+++	+++
C_{18}	+++	++	+++	−	±	+++	+++	++

Endogenous subtracted; +, ++, etc.: no. of +'s indicates degree of oxygen-uptake response on new substrate (μl/mg/hr after 4 hrs) under conditions cited in the text; ±: approx. the same as endogenous; −: O_2-uptake inhibited. See FIGS. 1–3 for detailed data on C_{16}-, C_{12}-, and glucose-exposed cells.

cells were tipped from the side arm into the main well. Flasks were shaken at 120 oscillations per minute and the temperature of the water bath was 25°.

EXPERIMENTAL RESULTS

C_8 to C_{14} acids inhibit O_2 uptake of glucose-exposed cells (FIG. 1). The C_2 to C_7 and C_{16} to C_{18} acids stimulate O_2 uptake and the values are considerably above the endogenous level. Moreover, O_2 uptake on C_6 and C_{18} is slightly above, and that on C_{16} significantly above the glucose level, the latter being the substrate on which the cells had previously been grown. Palmitate gave the best O_2-uptake response of the substrates tested.

Typical O_2 uptakes, for cells exposed to various fatty acid substrates, are presented in TABLE 1. Responses of cells exposed to other acids were also obtained; however, those omitted from the table show no marked deviations from the type of responses shown.

O_2-uptake responses by cells exposed to long-chain fatty acids (C_{16}–C_{18}) are remarkably similar. The general pattern of stimulation by C_2–C_7 and C_{16}–C_{18}, inhibition by C_8–C_{14}, described for glucose-exposed cells is again displayed, though with minor variations: (1) among the shorter-chain-length acids valerate and caproate provide an outstanding response; (2) both C_7 and C_8 acids give significant uptakes

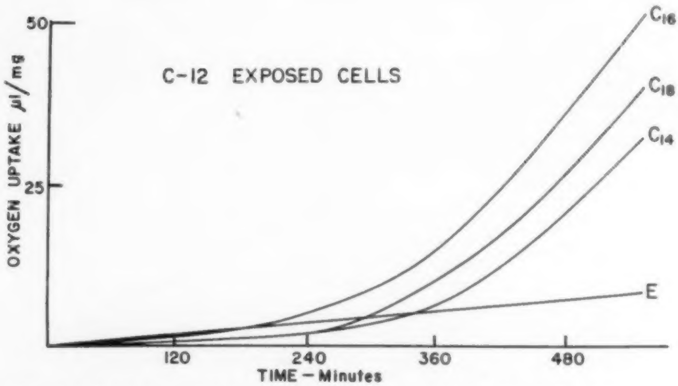

FIG. 2. Oxidation of fatty acids by laurate-exposed cells of *S. violacea*. Cup contents and conditions as indicated in the text. C_{18}, C_{16} and C_{14} refer to the fatty acid of the chain-length cited. E = endogenous uptake (without substrate). Except for C_{15}, fatty acids of all chain lengths from C_2 to C_{18} were tested; those not shown gave values below the endogenous rate.

with cells previously exposed to palmitate. While the responses to stearate and margarate were uniformly higher than endogenous rates, palmitate gave the best response to the cells exposed to any acid in the C_{16}–C_{18} chain length group.

Cells exposed to valerate and caproate show an unusual response to C_6 and C_7 substrates; the responses of valerate-exposed cells to C_5 and C_8 acids were also rather high (TABLE 1). Other than this, palmitate gave the highest readings for cells exposed to fatty acids with the shorter chains. Further, except for valerate-exposed cells, where C_8 stimulated, the pattern of inhibition by C_8–C_{14} substrates remains the same for cells exposed to any acid in the C_2–C_7 chain length group; the nature and

relative ratios between the stimulatory substrates are also much the same as for glucose-grown and C_{16}–C_{18}-exposed cells.

O_2-uptake responses are greatly reduced, even when usually stimulatory substrates are presented to C_9–C_{13}-exposed cells (TABLE 1). The long lag involved before any substrate gives values significantly above the endogenous level (FIG. 2) indicates the persistent nature of the inhibitory effect. After eight hours in this case with laurate-exposed cells, palmitate, stearate, and myristate were the only substrates where significant recovery from inhibition had taken place. O_2 uptake on all other substrates remained approximately at the endogenous value or markedly below (TABLE 1). After eight hours, in all cases after exposure to C_9–C_{13} substrates, palmitate gave the highest O_2-uptake response.

Comparison of the endogenous values obtained after exposure to the various substrates (TABLE 1, FIGS. 1–3) is also of interest. Relatively uniform and medium uptakes were found after exposure to those substrates which gave modest stimulation to glucose-grown cells (5.0–7.5 μl/mg/hr). The endogenous values were higher after exposure to substrates markedly stimulating glucose-grown cells (10.5–18.8 μl/mg/hr) and lower after exposure to substrates inhibiting them (approx. 1 μl/mg/hr). Thus the short-term responses (4 hr) of glucose-grown cells to fatty acids are similar in nature and degree to those found after exposures for longer periods (24 hr), indicating a persistent and perhaps basic nature to these relationships.

DISCUSSION

The above data suggest that the enzymes responsible for long-chain (C_{16}–C_{18}) fatty-acid oxidation are of a constitutive nature. On both glucose-grown and fatty-acid-exposed cells, palmitate, margarate and stearate start uptakes without lags, and throughout all experiments stand markedly above the endogenous rates. Usually the response is considerably above the values obtained for glucose oxidation by the same cells. Constitutive enzymes are also present to oxidize the acids with shorter chains, particularly evident in the C_5–C_7 range.

No evidence for the presence of constitutive enzymes oxidizing fatty acids in the C_9–C_{13} range has been disclosed. The pattern after exposure to these substrates, both with glucose-grown and fatty-acid-exposed cells, is a marked inhibitory one. Since the range of environmental variables for cells in contact with these substrates is almost infinite, and not all possibilities have been tested, it is impossible to state

unequivocally that such enzymes do not occur. However, the data suggest either (1) that this is unlikely, or (2) that any conditions under which C_9–C_{13} acids might possibly be oxidized would differ markedly from the conditions favorable for oxidation of similar substrates with both shorter and longer carbon chains.

Neither is there any evidence that C_9–C_{13} acids are metabolized

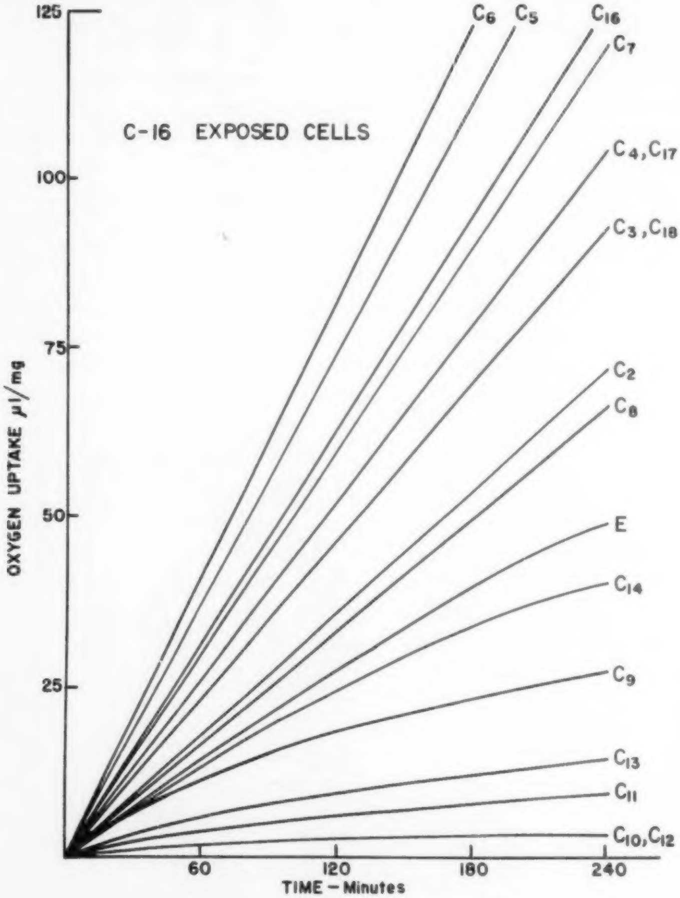

FIG. 3. Oxidation of fatty acids by palmitate-exposed cells of *S. violacea*. Cup contents and conditions as indicated in the text. C_{18}, C_{17}, C_{16}, etc., refer to the fatty acid of the chain-length cited. E = endogenous uptake (without substrate).

through adaptive pathways. In those cases where marked inhibitory substrates, such as caprate, undecanoate, laurate, etc., act on glucose-grown cells, or on cells exposed to normally stimulatory substrates, as stearate, palmitate, valerate, etc., the inhibitory pattern becomes more evident with time (FIG. 3). The curves representing O_2-uptake response start off at once with the highest slope they ever show and the curve then flattens out, indicating a gradually increasing inhibitory effect.

This pattern of inhibition by intermediate-chain-length substrates and stimulation by both shorter and longer chains is strikingly repeated regardless of the nature of the substrate to which adaptation had been attempted (TABLE 1). The pattern repeats that of the growth responses (Johnson, **1957**) and the results of previous O_2-uptake data from this mold (Johnson, **1958**). Further, cells exposed to the intermediate-chain-length substrates require more than four hours exposure to more favorable substrates to reverse the inhibitory effect (FIG. 2). The degree to which O_2 uptake is stimulated by C_{16}, C_8, C_5, and C_7 acids is sufficient to suggest the possibility of something unusual about these substrates in the fatty-acid metabolism of the mold. The short-chain acids giving the greatest response are just under one half the length of the long-chain acids giving the greatest response. Considering the inhibitory response in the C_9–C_{13} range, the data might suggest a splitting of the carbon chain when the longer-chain acids are metabolized, were there not chemical evidence (Dakin, **1908**) that oxidations at other points along the chain require more energy than at the β-carbons.

Recent studies (see Green, **1954**), based primarily on mammalian cells, have demonstrated that activation of fatty acids to form fatty-acyl CoA esters is the key initial step when these substrates are oxidized. After activation further metabolism proceeds rapidly and completely with β-oxidation cleavages forming successive C_2 fragments. The CoA thiol ester group is preserved on the longer residues until the final C_2 fragment is metabolized. Hence free fatty acids do not appear as intermediates in this scheme. The data from *S. violacea* are in line on this latter point; it is difficult to visualize free fatty acids of the C_5–C_{13} range as intermediates in long chain degradation by *S. violacea,* since they are so inhibitory both to growth and to O_2 uptake.

Should one assume that β-oxidation mechanisms operate in *S. violacea,* our data also suggest the possibility that at least two fatty-acid-activating enzymes (or sets of enzymes) are present in the cells, one of which activates the C_2–C_7 chains, the other C_{16}–C_{18} chains, but neither of which esterifies free fatty acids of the intermediate chains. This is an interesting possibility since the fatty-acid-acyl-CoA-activating enzymes

so far isolated from animal cells do possess some chain-length specificity. For example, a preparation from heart muscle activated only C_2 and C_3 acids (Beinert et al., **1953**); one from beef liver, the acids from C_4 to C_{12} (Mahler, **1953**); and a preparation from rat liver, C_{12} and above (Kornberg and Pricer, **1953**). Further experiments are currently in progress: (1) to investigate the metabolism of fatty-acyl CoA substrates by *S. violacea;* (2) to ascertain if the inhibition by C_9–C_{13} substrates is of the competitive type, and (3) to test for β-oxidation enzymes in cell-free extracts of the mold.

SUMMARY

(1) The enzymes oxidizing C_2–C_7 and C_{16}–C_{18} fatty acids in *Spicaria violacea* are of constitutive nature.

(2) Fatty acids of chain length from C_9 to C_{13} drastically inhibit O_2 uptake regardless of the substrates to which the cells have previously been exposed.

(3) The data suggest that at least two activating enzymes with an as yet undetermined specificity as to chain-length relationship are involved in fatty-acid oxidations by the mold.

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REFERENCES CITED

Beinert, H., D. E. Green, P. Hele, H. Hift, R. W. von Korff, and C. V. Ramakrishnan. 1953. The acetate activating enzyme system of heart muscle. Jour. Biol. Chem **203**: 35–45. *4 figs.*

Dakin, H. D. 1908. Comparative studies of the mode of oxidation of phenyl derivatives of fatty acids by the animal organism and by hydrogen peroxide. Jour. Biol. Chem. **4**: 419–435.

——. 1908. Further studies on the mode of oxidation of phenyl derivatives of fatty acids in the animal organism. Jour. Biol. Chem. **5**: 173–185; 303–309.

Green, D. E. 1954. Fatty acid oxidation in soluble systems of animal tissues. Biol. Rev. Cambridge Philos. Soc. **29**: 330–366. *2 figs.*

Johnson, G. T. 1957. Fatty acids as carbon sources for the growth of *Spicaria violacea.* Mycologia **49**: 172–177.

——. 1958. Oxidation of fatty acids by cell suspensions of *Spicaria violacea.* Mycologia **50**: 677–680.

Knoop, F. 1905. Der Abbau aromatischer Fettsäuren im Tierkörper. Beitr. Chem. Physiol. Path. **6**: 150–162.

Kornberg, A., and W. E. Pricer, Jr. 1953. Enzymatic esterification of α-glycerophosphate by long chain fatty acids. Jour. Biol. Chem. **204**: 345–357. *2 figs.*

Mahler, H. R. 1953. Role of coenzyme A in fatty acid metabolism. Fed. Proc. **12**: 694–702.

Melnick, D., F. H. Luckmann, and C. M. Gooding. 1954. Sorbic acid as a fungistatic agent for foods. VI. Metabolic degradation of sorbic acid in cheese by molds and the mechanism of mold inhibition. Food Research **19**: 44–58. *3 figs.*

Mukherjee, S. 1952. Studies on the degradation of fats by microorganisms. II. The mechanism of formation of ketones from fatty acids. Archiv. Biochem. Biophysics **35**: 23–33.

Silliker, J. H., and S. C. Rittenberg. 1951. Studies on the aerobic oxidation of fatty acids by bacteria. II. Application of the technique of simultaneous adaptation to the study of the mechanism of fatty acid oxidation in *Serratia marcescens*. Jour. Bact. **61**: 661–673. *5 figs.*

Stanier, R. Y. 1947. Simultaneous adaptation: a new technique for the study of metabolic pathways. Jour. Bact. **54**: 339–348. *6 figs.*

Stokoe, W. N. 1928. The rancidity of coconut oil produced by mould action. Biochem. Jour. **22**: 80–93.

Thaler, H., and G. Geist. 1939. Zur Chemie der Ketonranzigkeit. I. Über den Abbau gesättigter Fettsäuren durch *Penicillium glaucum*. Biochem. Zeit. **302**: 121–136. *4 figs.* II. Über die Bildung von Methylketonen aus β Oxyfettsäuren durch *Penicillium glaucum*. *Ibid.* 369–383.

SUSCEPTIBILITY OF GRAMINEAE TO TILLETIA CONTRAVERSA [1]

J. R. Hardison,[2] J. P. Meiners,[3] J. A. Hoffmann,[4] and J. T. Waldher [5]

Eleven grass species infected with *Tilletia contraversa* Kühn are here reported as additions to the world list of hosts for dwarf bunt. The new grass hosts [6] collected in the Pacific Northwest during 1958 are *Agropyron arizonicum, A. caninum, A. ciliare, A. mongolicum, Bromus carinatus, B. ciliatus, B. tomentellus, Festuca rubra* var. *commutata, F. ovina, F. ovina* var. *duriuscula,* and *Poa palustris.* Infection was also noted on *Bromus erectus* for the first time in North America. The fungus was identified previously on *B. erectus* in herbarium specimens from Czechoslovakia by Duran and Fischer (**7**), and Aebi (**2**) obtained infection on this grass by inoculation. Dwarf bunt on *P. palustris* represents the first report of infection on a species of the genus *Poa.* Spores from these specimens agree with the description for *Tilletia contraversa* originally proposed by Kühn (**19**) and the emended descriptions provided by Conners (**4**), Duran and Fischer (**7**) and Fischer (**10, 11**).

All of these grasses became infected in one or more tests seeded near Elgin, Oregon, Worley, Idaho, and Pullman, Washington, as indicated in Table 1.

Most of the infected grasses were seeded during May 1957, and the resulting plants were heavily inoculated during October with spores from wheat collected at the respective localities. Plants of *Agropyron arizonicum, A. ciliare, Bromus carinatus,* and *Poa palustris* became in-

[1] Cooperative investigations between the Crops Research Division, Agricultural Research Service, United States Department of Agriculture, and the Oregon, Washington and Idaho Agricultural Experiment Stations. Technical Paper No. 1174, Oregon Agricultural Experiment Station.

[2, 3, 4] Pathologists and [5] Agronomist, Crops Research Division, U. S. Department of Agriculture. Addresses: [2] Agric. Exper. Station, Corvallis, Oregon, [3] Plant Industry Station, Beltsville, Maryland, and [4, 5] Agric. Exper. Sta., Pullman, Washington. Grateful acknowledgment is made to the Soil Conservation Nursery Unit, U.S.D.A., Pullman, Wash., for providing seed of most of the grasses used in this study.

[6] Authorities for susceptible species are listed in Table 1. Taxonomy of grasses is taken from Hitchcock and Chase (**17**) unless otherwise stated.

fected only in row plantings that were seeded during October 1957 and to which dwarf-bunt spores were applied to the soil surface over the seed row immediately after planting.

Symptoms of infected plants were characteristic for dwarf bunt. Infected spikes of *Agropyron arizonicum, A. caninum, A. ciliare,* and *A. mongolicum* were broadened, and most of the culms were dwarfed one-third to two-thirds normal height. Infected panicles of the species of *Bromus, Festuca,* and *Poa* were compressed with thickened spikelets. The degree of culm dwarfing varied from extreme dwarfing—i.e., less than one-tenth normal—in *Agropyron arizonicum, Bromus ciliatus,* and *Poa palustris,* to only slight reduction in *Festuca ovina* var. *duriuscula.* Infected culms of most grasses were one-third to one-half normal height.

Dwarf bunt was found on several grasses during 1958 at new geographic locations as follows: Idaho: *Elymus glaucus, Festuca elatior,* and *F. rubra;* Washington: *Agropyron elongatum, A. trachycaulum, Arrhenatherum elatius,* and *Lolium perenne;* and Oregon: *E. glaucus.*

Because earlier host lists (**7**, **15**) do not contain the many new records, a revised list of the grasses susceptible to *Tilletia contraversa* with geographic locations and the original literature citations is presented in TABLE 1.

Possible additional host records in some of the reports from Europe have been omitted from this paper because of the present lack of agreement regarding identification of *Tilletia contraversa,* as explained by Fischer and Duran (**12**). Therefore, exclusion of uncertain host records from the list in Table I seems advisable until the identity of the smut fungi in such collections is clarified.

The host records listed for the Pacific Northwest by the writers were obtained primarily as a result of deliberate exposure of grass plants to dwarf-bunt infection. Beginning in 1952, grasses were planted in naturally infested soil each year at different locations. During 1956 and 1957 abundant dwarf-bunt spores were applied in October to crowns of spring-planted grasses and to the soil surface immediately after seeding other grasses in the fall.

During the first years (1952–54) of this study agriculturally important grasses likely to be planted in infested areas were tested for susceptibility to dwarf bunt. Testing of species outside the Tribe *Hordeae* was dictated by the outbreak of dwarf bunt on *Arrhenatherum elatius* (**14**) and *Festuca rubra* (**13**). More recently, the selection of grass species for tests of susceptibility to dwarf bunt was aided by the discovery of numerous new hosts for *Tilletia caries* (D.C.) Tul. resulting from seed inoculation with spores of 17 races of this fungus by Meiners

TABLE 1

HOST RANGE OF TILLETIA CONTRAVERSA

HOST SPECIES	GEOGRAPHIC LOCATION
Tribe *Hordeae*	
Aegilops cylindrica Host [a]	Iraq (**7**) [b], U.S.A.: Utah (**5**)
Aegilops triuncialis L.	Iraq (**7**)
Aegilops umbellata Zhuk. (**7**) [a]	Turkey (**7**)
Agropyron amurense Drob. (**28**)	U.S.A.: Washington (**23**)
Agropyron arizonicum Scribn. & Smith	U.S.A.: Oregon [c]
Agropyron caninum (L.) Beauv.	U.S.A.: Idaho, Oregon, Washington [c]
Agropyron ciliare (Trin.) Franch. (**20**)	U.S.A.: Washington [c]
Agropyron cristatum (L.) Gaertn.	Caucasus (**4**), Siberia (**7**), U.S.A.: Idaho, Oregon (**15**)
Agropyron dasystachyum (Hook.) Scribn.	U.S.A.: Oregon, Washington (**23**)
Agropyron desertorum (Fisch.) Schult.	U.S.A.: Idaho, Oregon (**15**)
Agropyron diazii Sennen (**7**)	Spain (**7**)
Agropyron elongatum (Host) Beauv. (**28**)	U.S.A.: Oregon (**13**), Washington [c]
Agropyron inerme (Scribn. & Smith) Rydb.	U.S.A.: Oregon (**22**)
Agropyron intermedium (Host) Beauv.	Caucasus, Europe (**4**), France (**26**), Switzerland (**1**), U.S.A.: Idaho (**10**) Oregon (**14**), Washington (**10, 23**)
Agropyron litorale (Host) Dum. (**4**)	Germany (**4**)
Agropyron mongolicum Keng (**28**)	U.S.A.: Oregon, Washington [c]
Agropyron orientale (L.) Roem. & Schult. (**4**)	Caucasus (**4**)
Agropyron repens (L.) Beauv.	Europe (**4**), Czechoslovakia, Denmark, Germany, Poland, Siberia, Yugoslavia (**7**), U.S.A.: Oregon (**23**)
Agropyron rigidum Beauv. var. *tomentosum* Regel (**4**)	Turkestan (**4**)
Agropyron riparium Scribn. & Smith	U.S.A.: Washington (**23**)
Agropyron sibiricum (Willd.) Beauv.	U.S.A.: Idaho (**15**)
Agropyron subsecundum (Link) Hitchc.	U.S.A.: Idaho (**10**), Oregon (**16**)
Agropyron trachycaulum (Link) Malte	U.S.A.: Idaho (**22**), Oregon (**16**), Washington [c]
Agropyron trichophorum (Link) Richt.	Persia (**7**), U.S.A.: Oregon (**22**)
Agropyron triticeum Gaertn. (**7**)	Siberia (**7**)
Elymus aralensis Regel (**7**)	Turkestan (**7**)
Elymus canadensis L.	U.S.A.: Idaho, Oregon (**16**)
Elymus crinitus Schreb. (**7**)	Greece (**7**)
Elymus glaucus Buckl.	U.S.A.: Idaho,[c] Oregon,[c] Washington (**23**)
Elymus sibiricus L.	Yugoslavia (**7**), U.S.A.: Oregon (**16**)
Elymus triticoides Buckl.	U.S.A.: Oregon (**23**)
Hordeum bulbosum L. (**17**)	Russia, Syria, Turkestan, Turkey, Yugoslavia (**7**)
Hordeum leporinum Link (**7**)	Algeria, Australia, Iran, Spain, Turkey (**7**)
Hordeum vulgare L.	Bulgaria, Iran, Iraq, Japan, Yugoslavia (**7**)
Lolium multiflorum Lam.	U.S.A.: Idaho (**16**), New York (**6**)
Lolium perenne L.	U.S.A.: New York (**6**), Washington [c]
Lolium remotum Schrank	Denmark (**7**)

TABLE 1—(*Continued*)

HOST SPECIES	GEOGRAPHIC LOCATION
	Tribe *Hordeae*
Secale cereale L.	Europe, Germany (**4**, **24**), Bavaria (**3**, **25**, **27**), Switzerland (**2**), Turkey (**12**), U.S.A.: Idaho, Montana (**16**), Oregon (**15**), Utah (**29**)
Triticum aestivum L.	Argentina, Canada, Europe, Iran, Italy, Persia, U.S.A.: California, Colorado, Idaho, Indiana, Michigan, Montana, New York, Oregon, Utah, Washington (**12**)
Triticum dicoccum Schrank	Switzerland (**2**)
Triticum spelta L.	Germany (**4**, **27**)
	Tribe *Aveneae*
Arrhenatherum elatius (L.) Presl	U.S.A.: Idaho (**16**), Oregon (**14**), Washington [c]
Koeleria cristata (L.) Pers.	U.S.A.: Oregon (**23**)
	Tribe *Festuceae*
Bromus carinatus Hook. & Arn.	U.S.A.: Oregon, Washington [c]
Bromus ciliatus L.	U.S.A.: Washington [c]
Bromus erectus Huds.	Czechoslovakia (**7**), Switzerland (**2**), U.S.A.: Oregon [c]
Bromus marginatus Nees	U.S.A.: Idaho (**16**), Oregon (**22**)
Bromus tomentellus Boiss. (**28**)	U.S.A.: Oregon [c]
Dactylis glomerata L.	U.S.A.: Oregon (**15**)
Festuca elatior L. (*F. pratensis* Huds.)	Germany (**24**), Switzerland (**2**), U.S.A.: Idaho,[c] Oregon (**16**)
Festuca idahoensis Elmer	U.S.A.: Oregon (**23**)
Festuca ovina L.	U.S.A.: Idaho [c]
Festuca ovina var. *duriuscula* (L.) Koch	U.S.A.: Oregon [c]
Festuca rubra L.	U.S.A.: Idaho,[c] Oregon (**13**)
Festuca rubra var. *commutata* Gaud.	U.S.A.: Idaho [c]
Poa palustris L.	U.S.A.: Washington [c]
	Tribe *Agrostideae*
Alopecurus myosuroides Huds. (**7**)	Italy (**7**)

[a] Taxonomy of grasses from Hitchcock and Chase (**17**) unless otherwise indicated by number reference to literature citation in parentheses.
[b] Numbers refer to literature cited.
[c] Collections described in present paper.

(**20**, **21**). During the last three years dwarf-bunt pathogenicity tests have included grass species reported to be susceptible to *T. caries* (**8**, **9**, **20**, **21**), because many grasses appear to be susceptible to both smut species. Particular attention was given to grasses susceptible to certain differential tester races of *T. caries*, susceptibility to which usually indicates probable susceptibility to dwarf bunt, *T. contraversa*, in wheat varieties (Holton et al., **18**) and in grasses (Meiners **20**, **21**).

Since 1955 the tests have included grass species that were important in dwarf-bunt-infested areas either as grass crops or weeds or were known to be susceptible to *Tilletia caries*. The important grass species not infected by *T. contraversa* during one to four years after they were planted in infested soil at three locations are listed in TABLE 2. Reaction to *Tilletia caries* also is listed for comparison.

TABLE 2

GRASSES NOT INFECTED AFTER EXPOSURE TO TILLETIA CONTRAVERSA

Grass species	Reaction to *T. caries*	Number of years planted					
		Oregon		Idaho		Washington	
		Time of planting					
		Spring	Fall	Spring	Fall	Spring	Fall
Agropyron spicatum (Pursh) Scribn. & Smith	S[a]	3[b,c]	3[b,c]	2	1[c]	1[c]	1[c]
Agrostis tenuis Sibth.	R	2[b]	2	—	1	—	—
Alopecurus arundinaceus Poir.	R	3[b,c]	—	1	1[c]	1[c]	1[c]
Alopecurus pratensis L.	R	3[b,c]	4[b,c]	1[c]	1	1[c]	1[c]
Bromus catharticus Vahl	R	2[b,c]	—	1[c]	1	—	—
Bromus inermis Leyss.	R	3[b,c]	4[b,c]	1	2[c]	1[c]	1[c]
Elymus giganteus Vahl	S	3[c]	1[c]	—	1	1[c]	1[c]
Elymus junceus Fisch.[d]	S	3[b,c]	4[b,c]	1[c]	2	1[c]	1[c]
Festuca arundinacea Schreb.	R	3[b,c]	3[b,c]	1[c]	1	1[c]	1[c]
Hordeum brachyantherum Nevski	S	3[b,c]	3[b,c]	1[c]	2	1[c]	1[c]
Phalaris arundinacea L.	R	3[b,c]	4[b]	1[c]	1	1[c]	1[c]
Phleum pratense L.	R	2[b]	1[c]	1[c]	2	1[c]	1[c]
Poa ampla Merr.	R	3[b,c]	3[c]	1[c]	2	1[c]	1[c]
Poa canbyi (Scribn.) Piper	R	2[c]	1[c]	—	—	1[c]	1[c]
Poa nevadensis Vasey ex Scribn.	R	3[b,c]	1[c]	1[c]	2	1[c]	1[c]
Poa pratensis L.	R	3[b,c]	4[b,c]	1[c]	2	1[c]	1[c]
Sitanion hystrix (Nutt.) J. G. Smith	R	1[c]	2[b,c]	1[c]	—	1[c]	1[c]

[a] R is Resistant and S is Susceptible, as listed by Meiners (**20**, **21**).
[b] Includes tests with spores applied to grass plants or seed row, October, 1956.
[c] Includes tests with spores applied to grass plants or seed row, October, 1957.
[d] Taxonomy from Weintraub (**28**).

Two additional species, *Agropyron semicostatum* (Steud.) Nees ex Boiss. and *Secale montanum* Guss., were planted in the spring and fall of 1957 at one location each in Oregon and Washington. *Hordeum jubatum* L. was planted in the fall of 1956 in Oregon. All of these plantings were inoculated in October by adding dwarf-bunt spores to the grass crowns or to the soil surface over the seeded row. However, no dwarf bunt appeared in these three grasses. *H. jubatum* is the only 1 of the 3 species known to be susceptible to *Tilletia caries*.

Resistance to *T. caries* in the several grasses listed in TABLE 2 suggests that these grass species also may be resistant to dwarf bunt, because practically all grass species that are susceptible to *Tilletia contraversa* are also susceptible to at least some races of *T. caries* (**20**, **21**). In the Pacific Northwest the number of grasses susceptible to both fungi far exceeds those that are infected by only one species. Hosts common to both species of *Tilletia* include 32 species of grasses, while 6 have been shown to be susceptible only to *T. caries* and 6 appear to be susceptible only to *T. contraversa*.

Certain grass species which are winter annuals and resistant to *Tilletia caries* (**20**, **21**) were free from dwarf bunt during 1958 after they were planted in infested soil and spores added to the surface of the soil over the seed row during October 1957 at one location each in Oregon and Washington. These grass species include: *Bromus brizaeformis* Fisch. & Mey., *B. commutatus* Schrad., *B. japonicus* Thunb., *B. mollis* L., *B. racemosus* L., *B. secalinus* L., *B. squarrosus* L., and *B. tectorum* L. No infection has been seen in a number of other grasses that were planted at different times and locations as follows: *Agrostis alba L.* (fall 1953, Idaho); *A. palustris* Huds. (fall 1952, Oregon); *Bromus arvensis* L. (fall 1952, Oregon); *B. purgans* L. (spring 1957, Idaho, Oregon, Washington; fall 1957, Washington); *Elymus dahuricus* Griseb.[7] (fall 1957, Oregon; spring and fall 1957, Washington); *Holcus lanatus* L. (spring and fall 1957, Oregon and Washington; *Stipa columbiana* Macoun (spring 1957, Oregon; spring and fall 1957, Washington); and *Stipa viridula* Trin. (spring 1957, Oregon and Washington). Grasses seeded in 1956 and 1957 were inoculated in October of each year. In addition to the experimental plantings *Bromus tectorum*, *Phleum pratense*, and *Poa compressa* L. were free from infection, although these grasses have been abundantly present as weeds in two of the Oregon plot areas each year (1952–58).

Despite the application during October 1957 of abundant spores to the soil over fall-planted seeds and to crowns of spring-planted grasses, very little dwarf bunt appeared during 1958 in numerous grasses. The one exception was *Agropyron caninum* in which 10 to 30 percent infected culms was noted at all locations. Other grasses known to be susceptible, especially *Agropyron elongatum*, *A. intermedium*, *A. trachycaulum*, *A. trichophorum*, *Arrhenatherum elatius*, *Festuca elatior*, and *F. idahoensis*, were included in the tests and were either free from smut or only one to four or five infected inflorescences appeared in rows, most

[7] Taxonomy from Weintraub (**28**).

of which contained several hundred healthy culms. In the same plots plants of the fall-sown susceptible wheat varieties Elgin and Alicel were severely infested at two locations in Oregon. Hydrid 128 was severely infested with dwarf bunt in Oregon and at Pullman, Washington. A very low incidence of infection in inoculated susceptible grasses also occurred during 1957 in experimental plantings at the same locations in contrast to heavy infection of the wheat varieties Elgin, Alicel and Orin.

The erratic appearance of the disease in grasses in all tests in the Pacific Northwest prevents classification of non-infected grass species as resistant to dwarf bunt. The low incidence of dwarf bunt in numerous plantings also precludes determination of the possible resistance of uninfected strains within various susceptible grass species. However, certain grasses that have not been infected after repeated exposure to *Tilletia contraversa* in nurseries planted in both spring and fall (TABLE 2) and that are known to be resistant to *T. caries* may be considered as reasonably safe crops to plant in dwarf-bunt-infested fields. The difficulty in obtaining infection of susceptible grasses by planting them in infested soil and by applying spores in the fall suggests that grasses are much less subject to severe attacks by the fungus than is winter wheat, *Triticum aestivum*.

The host range for dwarf bunt (TABLE 1) still must be regarded as incomplete, because many of the grasses that have been added to the host list each year were not infected in earlier trials. Thus, some grass species that have been exposed to infection for one to four years may still prove susceptible. Additional grass hosts for *Tilletia contraversa* are most likely to be found among the several grasses known to be susceptible to *T. caries* (**20**, **21**), including *Agropyron spicatum, Elymus giganteus, E. junceus, Hordeum brachyantherum, H. jubatum,* and *Sitanion jubatum*. However, infection of species in genera in addition to those listed in TABLE 1 may also be found.

Considering the wide range of susceptibility to dwarf bunt in the Gramineae (TABLE 1), it is surprising that so few infected grasses (**10**) were collected from the time dwarf bunt was first described in 1935 (**30**) until the first serious outbreak of the disease in cultivated grasses was observed in Oregon in 1952 (**14**). Aside from the fact that only limited attention was directed to susceptibility of grasses prior to 1952, the results of inoculation studies suggest that dwarf bunt probably was not prevalent on grasses in western United States. However, only limited plantings of grasses have been made on infested soil in this area.

SUMMARY

Dwarf bunt, *Tilletia contraversa* Kühn, was collected during 1958 for the first time on *Agropyron arizonicum* Scribn. & Smith, *A. caninum* (L.) Beauv., *A. ciliare* (Trin.) Franch., *A. mongolicum* Keng, *Bromus carinatus* Hook. & Arn., *B. ciliatus* L., *B. tomentellus* Boiss., *Festuca ovina* L., *F. ovina* var. *duriuscula* (L.) Koch, *F. rubra* var. *commutata* Gaud., and *Poa palustris* L., and for the first time in North America on *Bromus erectus* Huds. Infection of *P. palustris* represents the first record of dwarf bunt on a species of the genus *Poa*. The host range for dwarf bunt now includes *Aegilops* (3 species), *Agropyron* (22 species), *Alopecurus* (1 species), *Arrhenatherum* (1 species), *Bromus* (5 species), *Dactylis* (1 species), *Elymus* (6 species), *Festuca* (4 species and 2 varieties), *Hordeum* (3 species), *Koeleria* (1 species), *Lolium* (3 species), *Poa* (1 species), *Secale* (1 species), and *Triticum* (3 species). Scarcely more than a trace of infection was obtained on plants of several susceptible grasses planted in spring and fall several times during 1952–57 in infested soil and during 1956 and 1957 with spores added to plants or to the seed row in October at five different locations in Idaho, Oregon, and Washington. The general lack of infection in inoculated plots indicates that grass crops are much less subject to dwarf-bunt infection than is winter wheat, *Triticum aestivum* L.

LITERATURE CITED

1. **Aebi, H.** 1955. La carie naine du froment. Aspect actuel du problème en Suisse. Rev. Rom. Agric. **11**: 65–68.
2. ——. 1957. Zur Frage des Wirtsspektrums des Zwergbrandes. Bayer. Landwirts. Jahrb. **34**: 8–14.
3. **Böning, K.** 1955. Infektion von Roggen mit Zwergbrand des Weizens unter gewöhnlichen Freilandverhältnissen. Zeits. Pflanzenbau Pflanzensch. II. **6**: 225–228.
4. **Conners, I. L.** 1954. The organism causing dwarf bunt of wheat. Canad. Jour. Bot. **32**: 426–431.
5. **Dewey, W. G., and D. C. Tingey.** 1958. A new grass host for dwarf bunt. Pl. Dis. Rep. **42**: 18–19.
6. ——, **and L. J. Tyler.** 1956. Dwarf bunt on ryegrass in New York. Pl. Dis. Rep. **40**: 508.
7. **Duran, R., and G. W. Fischer.** 1956. Further studies on the synonymy and host range of the dwarf bunt fungus, *Tilletia contraversa*. Res. St. State Coll. Washington **24**: 259–266.
8. **Fischer, George W.** 1936. The susceptibility of certain wild grasses to *Tilletia tritici* and *Tilletia levis*. Phytopathology **26**: 876–886.
9. ——. 1939. Studies on the susceptibility of forage grasses to cereal smut fungi. III. Further data concerning *Tilletia levis* and *T. tritici*. Phytopathology **29**: 575–591.

10. ——. 1952. *Tilletia brevifaciens* sp. nov., causing dwarf bunt of wheat and certain grasses. Res. St. State Coll. Washington **20**: 11–14.
11. ——. 1953. Manual of the North American Smut Fungi. Ronald Press, New York. 343 pp.
12. ——, **and Ruben Duran.** 1956. Some new distribution and early incidence records of dwarf bunt of wheat and rye. Res. St. State Coll. Washington **24**: 267–274.
13. **Hardison, John R.** 1954. New grass host records and life history observations of dwarf bunt in eastern Oregon. Pl. Dis. Rep. **38**: 345–347.
14. ——, **and Malcolm E. Corden.** 1952. A serious outbreak of dwarf bunt in tall oat grass in Oregon. Pl. Dis. Rep. **36**: 343–344.
15. ——, **H. S. Fenwick, and J. P. Meiners.** 1955. Additional grass hosts and a revised host list for dwarf bunt. Pl. Dis. Rep. **39**: 685–687.
16. ——, **and J. P. Meiners.** 1956. New host records for dwarf bunt in the Pacific Northwest. Pl. Dis. Rep. **40**: 1058–1060.
17. **Hitchcock, A. S., and Agnes Chase.** 1950. Manual of the grasses of the United States. 1051 pp., 1199 illus. U. S. Dept. Agric. Misc. Publ. No. 200.
18. **Holton, C. S., R. H. Bamberg, and R. W. Woodward.** 1949. Tester races for dwarf bunt resistance factors in winter wheat varieties. Agron. Jour. **41**: 250–252.
19. **Kühn, J.** 1874. *Tilletia contraversa*. In L. Rabenhorst, Fungi europaei. Hedwigia **13**: 188–189.
20. **Meiners, Jack P.** 1956. Extension of the known grass host range for *Tilletia caries* by inoculation. Res. St. State Coll. Washington **24**: 331–336.
21. ——. Unpublished annual reports for 1956 and 1957.
22. ——, **J. T. Waldher, J. R. Hardison, and H. S. Fenwick.** 1956. Additions to the host range of dwarf bunt. Pl. Dis. Rep. **40**: 26–27.
23. ——, **and J. R. Hardison.** 1957. New host records for dwarf bunt in the Pacific Northwest. II. Pl. Dis. Rep. **41**: 983–985.
24. **Niemann, E.** 1957. Über den Wirtsbereich der Steinbrandarten von Getreide und Gräsern. Bayerisches Landwirtschaftliches Jahrbuch. **34**: 6–7.
25. **Stauber.** 1955. Zwergbrand an Weizen und Winterroggen im Landkreis Sulzbach-Rosenberg. Pflanzenschutz **7**: 164. (Abstract in Rev. Appl. Mycol. **35**: 173. 1956.)
26. **Viennot-Bourgin, G., and Jeannine Zieglé.** 1952. La carie des grains de seigle en France. Comptes Rendus Acad. Agric. Fr. **18**: 729–730.
27. **Warmbrunn, K.** 1952. Untersuchungen über den Zwergsteinbrand. Phytopathol. Zeits. **19**: 441–482.
28. **Weintraub, Frances C.** 1953. Grasses introduced into the United States. U. S. Dept. Agric., Forest Service, Agriculture Handbook No. 58. 79 pp.
29. **Woodward, R. W., C. S. Holton, and O. A. Vogel.** 1952. Dwarf bunt in rye. Pl. Dis. Rep. **36**: 434.
30. **Young, P. A.** 1935. A new variety of *Tilletia tritici* in Montana. (Abstract.) Phytopathology **25**: 40.

A PRELIMINARY SURVEY OF THE GYMNOASCACEAE. II.

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This is the final part of a two-paper series in which is presented a preliminary survey of the Gymnoascaceae. Although the writer is still engaged in a long-range research project concerned with this little known family of fungi, it seems advisable to present a complete survey of the family as it is now constituted, and then make changes, additions and corrections in the future as more information is accumulated. The first paper in this series (Kuehn, **1958**) presented keys to the genera within the Gymnoascaceae, as well as keys to the species of all the genera with two exceptions, followed by descriptions of these species. The two genera not discussed in the previous paper, but which are presented in the present treatment, are *Gymnoascus* and *Myxotrichum*.

GYMNOASCUS Baranetzky, Bot. Zeit. **30**: 158. 1872.
Myrillium Clem. in Clem. & Shear, Gen. Fung. 246. 1931.

Cleistothecia more or less globose, usually white or in light or bright colors, rarely darker. Peridial hyphae loosely reticulate, anastomosed, thick-walled, septate, smooth or asperulate, with many free apices, either spine-like or elongate septate branches which terminate in short, pointed or obtuse, straight or slightly curved branchlets. Asci globose, subglobose or obovate, usually 8-spored, wall evanescent. Ascospores hyaline or brightly colored or tinged brown, globose, oblate, elliptical or lenticular, smooth or sculptured. Asexual phase present or absent.

TYPE species: *Gymnoascus reessii* Baranetzky.

KEY TO THE SPECIES OF GYMNOASCUS

A. Ascocarps dark, black or brown or shades of red-brown .... B
AA. Ascocarps light or brightly colored .... H
B. Long spine-like appendages with 2, 3 or 4 short branchlets in whorls; ascocarps dark-brown to black C
BB. Appendages not long and spine-like, and without whorls of branchlets; ascocarps greenish, brown to red-brown or yellow-brown .... D
C. Ascocarp black-brown or dark-brown; appendages with 2–3 opposite or whorled branchlets; ascospores sub-fusoid, hyaline .... 1. *G. setosus*

CC. Ascocarp deep-brown; appendages with verticels of 4 branchlets; ascospores globose, dark, small, 2.5 μ diam. .... 2. *G. verticillatus*

D. Ultimate apices of peridial hyphae not hyaline .... E

DD. Ultimate apices of peridial hyphae often hyaline .... F

E. Ascocarps red-yellow, red-brown, orange-red or yellow-brown; ascospores globose, 2.8–4.2 μ diam., or ovoid, light-yellow to pale-brown; appendages with short, lateral branchlets .... 3. *G. reessii*

EE. Ascocarps brown or greenish; ascospores globose or navicular; appendages rigid, straight spines .... 4. *G. brevisetosus*

F. Ascocarps brown; ascospores globose; appendages 11.9–38 μ long; asci not stipitate .... G

FF. Ascocarps ashy-green; ascospores navicular; appendages up to 100 μ long; asci stiped, with stipes 9–12 μ long .... 5. *G. stipitatus*

G. Ascocarp brown, 300–400 μ diam.; peridial hyphae granular; asci 10–12 μ diam. .... 6. *G. umbrinus*

GG. Asocarp red-yellow-brown, up to 500 μ diam.; peridial hyphae almost smooth; asci 7–8 μ diam. .... 7. *G. subumbrinus*

H. Ascocarps white and remaining almost so throughout development I

HH. Ascocarps becoming shades of red, yellow or orange .... K

I. Peridial hyphae granular, ending in long spirals; ascospores globose, small, less than 3.0 μ diam. .... 8. *G. racovitzae*

II. Peridial hyphae not terminating in spirals; ascospores not spherical, larger than 3.0 μ .... J

J. Asci multispored, measuring 20 × 45 μ; ascospores 2 × 6 μ .... 9. *G. myriosporus*

JJ. Asci 8-spored, 7–8 μ diam.; ascospores 3 × 4.5 μ .... 10. *G. gypseus*

K. Ascocarps in shades of red L

KK. Ascocarps lacking red shades .... O

L. Asci large, 12–13 μ diam.; ascospores large, above 5.0 μ in largest dimension .... M

LL. Asci smaller, 11.4 μ diam. or less; ascospores smaller, up to 4.2 μ in greatest dimension .... N

M. Ascocarps red-yellow (golden); ascospores globose to sublenticular, 4–4.5 × 5–6 μ .... 11. *G. confluens*

MM. Ascocarps brick-red; ascospores lenticular, 6.4 μ diam. ...... 12. *G. reticulatus*

N. Asci 8.4–11.4 μ diam.; peridial hyphae smooth or asperulate; ascospores globose, 2.8–4.2 μ diam., or ovoid, light-yellow to pale-brown .... 3. *G. reessii*

NN. Asci 7–8 μ diam.; peridial hyphae almost smooth; ascospores hyaline to tawny, globose, 3–4 μ diam. .... 7. *G. subumbrinus*

O. Ascocarp pale-yellow, 330–500 μ diam.; asci large, 15–18 μ diam.; ascospores hyaline, globose, 4–6 μ diam. .... 13. *G. zuffianus*

OO. Not with the above combination of characters .... P

P. Ascocarp at first white, then yellow-white; asci 8–9 μ diam.; ascospores globose to subglobose, hyaline, 3.5–4.5 μ diam. .... 14. *G. ossicola*

PP. Not with the above combination of characters .... Q

Q. Ascospores smooth .... R

QQ. Ascospores warty, not smooth .... S

R. Ascocarp red-yellow (golden); asci 12–13 μ diam.; ascospores globose to sublenticular, 4–4.5 × 5–6 μ .... 11. *G. confluens*

RR. Ascocarps red-brown, red-yellow, orange-red or yellow-brown; asci 8.4–11.4 μ diam.; ascospores globose, 2.8–4.2 μ diam.; or ovoid, 1.4–2.8 × 2.8–4.2 μ, light-yellow to pale-brown .... 3. *G. reessii*

S. Ascospores rough-warty, hyaline or tinged yellow, oval, 2.5–3 × 5–6 μ, mycelium white and ascocarp yellow; asci 9–10 μ diam. ...... 15. *G. bourquelotii*

SS. Ascospores minutely warty, hyaline or tinged yellow, oval, 2.5–3 × 5–6 μ, mycelium and ascocarp yellow; asci 12–15 μ diam. .... 16. *G. flavus*

1. G. SETOSUS Eidam, Bot. Centr. **10**: 107. 1882.

Cleistothecia more or less globose, dark-brown to brown-black. Peridial hyphae thick-walled, brown-black, branching repeatedly, all branches terminating in a sharp point, spine-like, and bearing 2–3 opposite or whorled, short, sinuous branchlets. Asci very numerous, forming a snow-white interior mass, oval or subglobose, 7–8 μ diam. Ascospores hyaline, fusoid to sub-fusoid, 2.0 × 5–7 μ.

TYPE LOCALITY: Germany.

HABITAT: Old bees' nest, soil.

DISTRIBUTION: Germany, England.

ILLUSTRATIONS: Massee and Salmon, Ann. Bot. **16**, *pl. 4, f. 18–22;* Dale, Ann. Bot. **17**, *f. 33–39.*

The above description was adapted from those of Schroeter (**1893**) and Massee and Salmon (**1902**). The writer received a culture of *G. setosus* from the Centraalbureau voor Schimmelcultures. This culture fruits very weakly, but the writer has not had the opportunity to examine it more closely. *Gymnoascus setosus* was considered to be conspecific with *Eidamella deflexa* by C. W. Dodge (**1935**), but DeLamater (**1937**) presented an analysis of these two species and showed them to be distinct. On the original drawings of Massee, now located in the herbarium of the New York Botanical Garden, the name *Myxotrichum setosum* occurs as a synonym for *G. setosus.*

2. G. VERTICILLATUS A. L. Smith, Brit. Myc. Soc. Trans. **1**: 154. 1896.

Cleistothecia more or less globose. Peridial hyphae loosely intertwined, deep-brown, thick-walled, the outer ends free and bearing a series of regular verticels of 4 curved, blunt branchlets up to 15 μ long, 5 μ wide. Asci evanescent, the groups of ascospores oblong, 10 × 7 μ. Ascospores dark-colored, globose, small, about 2.5 μ diam.

TYPE LOCALITY: England.

HABITAT: Bones of dead rabbit buried for one year.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Smith, Jour. Roy. Micr. Soc. **1900**, *pl. 3, f. 2.*

This description is taken from those of Smith (**1896**, **1900**).

3. G. REESSII Baranetzky, Bot. Zeit. **30**: 158. 1872.

Myxotrichum coprogenum Sacc., Michelia **2**: 372. 1881; Syll. Fung. **4**: 319. 1886.

M. coprogenum var. *malacense* Sacc. and Paol. Myc. Malac. n. 120; Sacc. Syll. Fung. **10**: 593. 1892.

M. ochraceum Berk. and Br. (Grev. **3**: 184. 1874),* *coprogenum* Sacc., Michelia **2**: 372. 1881.

Cleistothecia spherical, red-brown, red-yellow, orange-red, or yellow-brown, 189–500 μ diam. Peridial hyphae smooth or asperulate, thick-walled, shades of red or yellow, septate, anastomosed and intertwined, bearing short appendages, simple or branched, straight or curved, acute or blunt. Asci hyaline, obovate to subglobose, 8.4–11.4 μ, 8-spored, wall evanescent. Ascospores smooth, light-yellow, red-brown or pale-brown, globose and 2.8–4.2 μ diam., or ovoid and 1.4–2.8 $\times$ 2.8–4.2 μ, but with much strain variation in ascospore dimensions. Racquet mycelium present. Asexual spore phase unknown.

TYPE LOCALITY: Leipzig, Germany.

HABITAT: Dung of sheep, horse, goat, rat, rodents, rabbit, coyote, deer, man, fowl, lemming, Canada goose; dead pupa of *Sphinx gallii*, soil.

DISTRIBUTION: Germany, England, Italy, Holland, Switzerland, Israel, North Africa, Belgium, Malacca, Manitoba and Quebec (Canada), Greenland, Illinois, Massachusetts, California, Ohio.

ILLUSTRATIONS: Baranetzky, Bot. Zeit **30**, *pl. 3, f. 1–26;* Benjamin, Aliso **3**, *pl. 7, f. 1–4;* Massee and Salmon, Ann. Bot. **16**, *pl. 4, f. 35–37;* Kuehn, Mycologia **48**, *f. 1–12, 30;* Dale, Ann. Bot. **17**, *f. 1–32;* Brefeld, Untersuch. **9**, *pl. 1, f. 40–44;* Eidam, Cohn Beitr. Biol. Pfl. **3**, *pl. 13, f. 25–26;* Massee, Brit. Fung. Flora **4**: 12, *f. 45;* Stoppel, Flora **97**: 342, *f. 3;* Fischer, E. and P., Nat. Pflanzenfam. **1** (1): 295, *f. 210;* Lindau, Krypt.-Fl. Brandenb. **7**: 74, *f. 17, 1–3;* Luerssen, Handb. Syst. Bot. 137, *f. A;* Winter, Krypt.-Fl. **2**: 12; Clements and Shear, Gen. Fung., *pl. 6, f. 4.*

The above description was taken primarily from Kuehn (**1956**), but the descriptions of Baranetzky (**1872**), Schroeter (**1893**), Massee (**1895**) and Massee and Salmon (**1902**) were also considered. The synonymy of *G. reessii* was discussed by Massee and Salmon (**1902**). Saccardo sent specimens of *Myxotrichum coprogenum* and *M. copro-*

genum var. *malacense* to Massee, who recognized them as representing *G. reessii.* Ferro (**1907**) examined the species of *Myxotrichum* in Saccardo's herbarium. He stated that *M. coprogenum* and its variety in reality represented *G. reessii.* According to Massee and Salmon, not only does *M. ochraceum* represent *M. deflexum* (now known as *Eidamella deflexa*) in part and *M. aeruginosum* in part (see Kuehn, **1958**), but also part of *M. ochraceum* might be in *G. reessii* because "Saccardo has described in Michelia **2**: 372, 1881, a fungus under the name of *M. ochraceum,* B. and Br., Grev. 1874, p. 184, * *coprogenum.* In Syll. Fung. **4**: 319, 1886, Saccardo described the species as *M. coprogenum,* Sacc., nec *M. ochraceum,* B. and Br."

Hennings (**1903**) described *Gymnoascus reessii* var. *deilephilae,* which was quite distinguishable in external appearance from *G. reessii* but which variation Hennings thought might be due to the unusual substrate. This fungus was isolated in Bruchmuhle, Germany, July 1901, from dung of a caterpillar, *Deilephila euphorbiae.* Peridial hyphae 3–$4\frac{1}{2}$ μ diam., yellow-gold, granulated, filled with yellow oil drops. The end branches of the peridial hyphae only stick out sparingly, and are very seldom short, hooked branches as in cases of typical *G. reessii.* Asci oval or elliptical, $6–10 \times 6–8$ μ, 8-spored. Ascospores almost spherical, or wide-ellipsoid, with one oil droplet, $3–4 \times 3–3\frac{1}{2}$ μ, smooth, yellowish.

4. G. BREVISETOSUS Kuehn, Mycologia **48**: 813. 1956

Cleistothecia spherical, brown, 315–555 μ diam. Peridial hyphae septate, cuticularized, asperulate, 4.5–5.8 μ diam., with appendages of sharp spines, unbranched, smooth or asperulate, 2.8–4.2 μ diam. at the base, 11.9–38 μ long. Asci obovate, hyaline, $5.6–7 \times 7–8.4$ μ, 8-spored, wall evanescent. Ascospores hyaline, smooth, spherical, 2.7–3.0 μ diam. Oidia hyaline, $1.2–1.6 \times 2.8–8.2$ μ. Odor distinct, musty or earthy.

TYPE LOCALITY: Texas.
HABITAT: Soil.
DISTRIBUTION: Known only from the type locality.
ILLUSTRATIONS: Kuehn, Mycologia **48**: *f. 13–29, 31.*
The above description is adapted from the original (Kuehn, **1956**).

5. G. STIPITATUS Lindfors, Svensk Bot. Tidskr. **14**: 270. 1920.

Cleistothecia ashy-green on filter paper moistened with inorganic salt solution, globose, 400–500 μ diam. Peridial hyphae thick-walled, dark-brown, septate, up to 3.5 μ diam., with end branches (appendages) ex-

tending radially. Appendages straight, rigid, up to 100 μ long, acuminate and tapering evenly to a point. (The distance between the apices of two adjacent spines is 400–500 μ.) Ascus clump colorless, 175–200 μ diam. Each ascus with a spherical, spore-containing part, 7–8 μ diam., and a stalk measuring $9–12 \times 1–1.5$ μ, and swollen bulb-like at the base. Ascospores 8 per ascus, hyaline, navicular (cymbiform), apiculate at both ends, and measuring $2.5–3 \times 4–5$ μ.

TYPE LOCALITY: not stated (probably Sweden).

HABITAT: Soil.

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Lindfors, Svensk Bot. Tidskr. **14**, *f. 1–3.*

The above description is taken from the original (Lindfors, **1920**).

6. G. UMBRINUS Boudier, Bull. Soc. Myc. Fr. **8**: 43. 1892.

Cleistothecia globose, 0.3–0.4 mm diam., at first white, then brown. Peridial hyphae dichotomously branched, septate and slightly thickened at bases of septa, tawny-colored, 5–6 μ diam., granular on exterior, thinned toward apices; ultimate apices hyaline. Internal hyphae very thin, septate, lax. Asci ovate or globose, 10–12 μ diam., 8-spored. Ascospores globose, hyaline or yellow, smooth, 3–4 μ diam.

TYPE LOCALITY: France.

HABITAT: On *Melolontha vulgaris* (June bug) attacked by *Botrytis tenella.*

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Boudier, Bull. Soc. Myc. Fr. **8**, *pl. 6, f. 2.*

The above description is based on that of Boudier (**1892**). The writer has obtained a culture of this species from the Centraalbureau voor Schimmelcultures but has not yet had opportunity to examine it.

7. G. SUBUMBRINUS A. L. Smith, Brit. Myc. Soc. Trans. **5**: 424. 1917.

Cleistothecia globose, up to 500 μ diam., red-yellow-brown. Peridial hyphae irregularly branched, often anastomosing, loose, brown, septate, 4–5 μ diam., almost entirely smooth, with the ultimate apices occasionally hyaline. Asci globose, plainly tawny, 3–4 μ diam.

TYPE LOCALITY: Chiswick, England.

HABITAT: Soil containing a caterpillar, soil.

DISTRIBUTION: England.

ILLUSTRATIONS: None.

This description is adapted from the original description of Smith and Ramsbottom (**1917**).

8. G. RACOVITZAE Lagarde, Arch. Zool. Expér. Génér. **53**: 281. 1913.
Myxotrichum racovitzae Lag., Arch. Zool. Expér. Génér. **53**: 280. 1913.

Fruiting bodies white, 0.5–2 mm diam., cottony, sessile to short-stalked. Peridial hyphae loosely intertwined, cylindrical, 2–3 μ diam., hyaline, septate, often granular, much branched, ending in long spirals. Asci 8-spored. Ascospores spherical, small, 1.5–3.0 μ diam., containing 1–4 oil droplets.

TYPE LOCALITY: France.
HABITAT: Woody fragments and decayed insects in a cave.
DISTRIBUTION: Known only from the type collection.
ILLUSTRATIONS: Lagarde, Arch. Zool. Expér. Génér. **53**, *pl. 12, f. 1–6.*
This description is taken from that given by Saccardo, **24**(2): 1146. 1928.

9. G. MYRIOSPORUS Rostrup, Med. om Groenland **18**: 12. 1894.
Myrillium myriosporus (Rost.) Clem. in Clem. & Shear, Gen. Fung., p. 246. 1931.

Ascocarps globose, white, floccose, 0.5–1 mm diam. Asci 20 × 45 μ, multisporous. Ascospores 3 × 6 μ.

TYPE LOCALITY: Denmark.
HABITAT: Claws of predatory birds; bird dung.
DISTRIBUTION: Known only from the type collection.
ILLUSTRATIONS: None.
This description is taken from that of Saccardo, **11**: 438. 1895. This species was placed in a new genus by Clements on the basis of the multisporous asci. The writer has seen only the account given by Saccardo, and until the species is re-isolated its position cannot be established.

10. G. GYPSEUS Nannizzi, Atti R. Accad. Fis. Siena X. **2**: 94. 1927.
Achorion gypseum Bodin, Ann. Derm. Syph. **8**: 585. 1907.
Sabouraudites gypseus (Bodin) Ota and Lang., Ann. Parasitol. Hum. Comp. **1**: 328. 1923.
Microsporum gypseum (Bodin) Guiart and Grigorakis, Lyon méd. **141**: 377. 1928.

Ascocarp globose, white, 0.66–1 mm diam. Peridial hyphae loosely intertwined, 4–5 μ diam., septate, hyaline, smooth, arcuate, simple or dichotomous, or rarely with unilateral, finely echinulate branches. Asci

in racemes, globose or oval, 7–8 μ diam., sessile or short stipitate, wall evanescent, 8-spored. Ascospores conglobate, oval, smooth, hyaline, 3.0×4–5 μ. Oidia, chlamydospores and fuseau present.

TYPE LOCALITY: France.

HABITAT: Cutaneous lesions on cheek of human female.

DISTRIBUTION: France, Italy.

ILLUSTRATIONS: Dodge, Med. Mycol., p. 427, *f. 73, 1–2;* Nannizzi, Atti R. Accad. Fis. Siena **2**, *f. 2, a–c;* Bodin, Ann. Derm. Syph. **8**, *f. 1–3, pl. 5, f. 1–7.*

This description is taken from that given by Dodge (**1935**), and is presented here in spite of the strong possibility that it should not be considered a perfect, ascosporic form. Nannizzi grew this species on substrates of animal origin, such as leather and feathers, and reported the production of asci. However, he presented no figures, and his rather poor analysis makes the work questionable. Tate (**1929**) could not duplicate the results obtained by Nannizzi. Nannizzi has been a staunch proponent of the thesis that the dermatophytes should be considered to be representatives of the Gymnoascaceae which have lost their ability to produce fertile asci (**1926**). Therefore, a complete reinvestigation of the species in question must be accomplished in order to establish the validity of his claims. The inclusion of *G. gypseus* in this treatment is done not out of a conviction that this is its natural position, but rather to indicate an area which is in need of further investigation.

11. G. CONFLUENS Sartory and Bainier, Bull. Soc. Myc. Fr. **29**: 261. 1913.

Ascocarps red-yellow (golden), often confluent to form masses up to 1 cm diam. Peridial hyphae hyaline, extremely delicate. Asci 12–13 μ diam., 8-spored, globose. Ascospores smooth, globose to sublenticular, 4–4.5×5–6 μ. Chlamydospores in series, spherical, red or red-brown. Mycelium hyaline, subdichotomously branched. Colonies developing a characteristic red-orange pigment. Mycelial hyphae colorless.

TYPE LOCALITY: France.

HABITAT: Dog dung; petals of a chinese aster.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Sartory and Bainier, Bull. Soc. Myc. Fr. **29**, *pl. 12.*

This description is based on those presented by Sartory and Bainier (**1913a**, **1913b**) and Saccardo (**24**(2): 1145. 1928). It is apparent from the original description that this species is similar to *Byssochlamys* or *Pseudoarachniotus* in the structure of the so-called ascocarp. The

original authors state that older fruiting bodies consist of nothing but asci, with no hyphae of any type evident. Such a situation is found in *B. nivea* and *P. roseus*. However, until more isolates of Gymnoascaceae are studied it is perhaps best to consider *G. confluens* as a species of *Gymnoascus* in this preliminary treatment. While the original description does not describe the color of the ascospores, it is evident that they are red-orange from the statement that older fruiting bodies are red-orange but consist of no structures others than asci plus ascospores.

12. G. RETICULATUS Zukal, Verhandl. Zool.-Bot. Ges. Wien **37**: 40. 1887.

Ascocarps subglobose to globose, brick-red, about 500 μ diam. Peridial hyphae loosely reticulate, septate, 5 μ diam., but swollen at the septa, rough, red, with very short, straight appendages. Asci short pedicellate, almost globose to spherical, 12–13 μ diam., 8-spored, wall evanescent. Ascospores ellipsoid to lenticular, thick-walled, yellow, about 6.4 μ diam. (A red *Torula*-like conidial form may be the imperfect stage.)

TYPE LOCALITY: Vienna, Austria.

HABITAT: Decaying horns and hooves of cows.

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Zukal, Verhandl. Zool. Bot. Ges. Wien **37**, *pl. 1, f. 5.*

This description is adapted from the descriptions of Saccardo (**1889**) and Zukal (**1887**).

13. G. ZUFFIANUS Morini, Mem. R. Accad. Sci. Bologna IV. **10**: 205. 1889.

Ascocarp globose, pale-yellow, about 300–500 μ diam. Appendages many, scattered, stiff, rigid and pointed. Asci globose, 15–18 μ diam., 8-spored. Ascospores hyaline, spheroid, 4–6 μ diam.

TYPE LOCALITY: Sassari, Sardinia.

HABITAT: On rotten wood.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Morini, Mem. R. Accad. Sci. Bologna IV. **10**, *f. 1–6.*

The above description is adapted from that presented by Saccardo (**10**: 71. 1892) and Morini (**1889**).

14. G. OSSICOLA Rostrup, Bot. Tidsskr. **21**: 45. 1897.

Ascocarp subspherical to spherical, up to 3 mm diam., at first white then yellow-white. Peridial hyphae intricately branched, septate, un-

cinate, hyaline, 2 μ diam. Asci short pedicellate, subglobose, 8–9 μ diam., 8-spored, wall evanescent. Ascospores subglobose to globose, hyaline, with one oil globule in the center, 3.5–4.5 μ diam.

TYPE LOCALITY: Denmark.

HABITAT: Bones of *Rhea americana*.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: None.

The description is based on those of Rostrup (**1897**) and Saccardo (**14**: 824. 1899).

15. G. BOURQUELOTII Boudier, Bull. Soc. Myc. Fr. **8**: 44. 1892.

Cleistothecia globose, 0.7–1 mm diam., yellow-gold. Peridial hyphae thin, rigid, dichotomously branched, golden, 4–5 μ diam., sparingly septate, granular, apices of appendages hyaline. Asci globose to irregularly ovate, 9–10 μ diam., 8-spored. Ascospores hyaline to translucent, elliptical to fusoid, 3–4 × 5–6 μ, regularly and linearly tuberculate with the tubercles arranged in 4 longitudinal rows. Imperfect stage unknown. Vegetative hyphae white.

TYPE LOCALITY: France.

HABITAT: Cotton wetted with nutritive liquid, seeds of cotton plant.

DISTRIBUTION: France, Pakistan.

ILLUSTRATIONS: Boudier, Bull. Soc. Myc. Fr. **8**, *pl. 6, f. 3.*

This description is adapted from those of Boudier (**1892**) and Saccardo (**11**: 437. 1895).

16. G. FLAVUS Klocker, Hedwigia **41**: 80. 1902.

Fruiting body yellow, globose, up to 1 mm diam. Peridial hyphae forming a loose web. Asci usually oval, rarely globose, 12–15 μ diam., 8-spored, wall evanescent. Ascospores oval, minutely warty, 2.5–3 × 5–6 μ, water-gray or weakly yellow. Conidia round or oval, rarely pyriform, 4.5–5 μ long, water-gray, constricted off in chains on lateral branches, rarely on terminal branches, subterranean, never aerial. Vegetative hyphae at first white, then yellow.

TYPE LOCALITY: Carlsberg, Denmark.

HABITAT: On a fly, *Lucilia caesar*.

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Klocker, Hedwigia **41**, *pl. 2;* Klocker, Bot. Tidsskr. **25**, *f. 1–5;* Klocker, Rev. de Myc. **25**, *pl. 229, f. 4–8.*

The above description was adapted from those of Klocker (**1902a**, **b**, **c**, **1903**) and Saccardo (**18**: 195. 1906).

EXCLUDED SPECIES

GYMNOASCUS AURANTIACUS (Peck) Saccardo, Syll. Fung. **8**: 823. 1889.
Gymnascella aurantiaca Peck, Jour. Myc. **1**: 57. 1885.
Myxotrichum aurantiacum (Peck) Sacc., Syll. Fung. **4**: 319. 1886.

This species was the type for a new genus *Gymnascella* proposed by Peck to include forms lacking discrete cleistothecia. Although Saccardo included it first in *Myxotrichum* and later transferred it to *Gymnoascus*, if the fungus has no peridium it must properly be assigned to *Pseudoarachniotus* or *Byssochlamys*. It is possible that this same species has been described as a species of *Arachniotus* as interpreted by Schroeter, but no published description seems to indicate synonymy.

G. DURUS Zukal, Ber. Deutsch. Bot. Ges. **8**: 295. 1890.

The three-layered peridium described by Zukal would place this species in the Eurotiaceae.

G. EIDAMI Cocconi, Mem. R. Accad. Sci. Bologna V. **2**: 32. 1891.

According to Saccardo (**10**: 71. 1892), the parenchymatous peridium of this species places it in the Eurotiaceae, preferably in *Cephalotheca*. An examination of Cocconi's illustrations as well as his description of the peridium of this species leads the writer to consider this species as not belonging to the Gymnoascaceae.

G. LUTEUS (Zukal) Saccardo, Syll. Fung. **11**: 437. 1895.

Penicillium luteum Zuk., Sitz.-Ber. Akad. Wien **98**: 561. 1889.
Talaromyces luteus (Zuk.) C. R. Benjamin, Mycologia **47**: 681. 1955.

Zukal described this species as a member of the genus *Penicillium*. Later, Saccardo, basing his opinion upon the available literature, transferred this species to *Gymnoascus*. For a discussion of the affinities of this species see Raper and Thom (**1949**) and Benjamin (**1955**). The entire complex of species now placed in *Talaromyces, Arachniotus, Byssochlamys* and *Pseudoarachniotus* must be thoroughly studied before a final arrangement can be attained. Until such studies have been completed, this species is regarded as *Talaromyces luteus* by the writer.

G. SUDANS Vailionis, Vyt. Didziojo Univ. Mat. Gamtos Fak. Darbai **11**: 115. 1936, = *Byssochlamys nivea* Westling.

This species has been discussed under *Byssochlamys nivea* (Kuehn, **1958**) and the synonymy was presented at that time.

G. UNCINATUS Eidam, Beitr. Biol. Pfl. **3**: 292. 1880, = *Myxotrichum uncinatum* (Eidam) Schroet.

A full discussion of this species is reserved for the section on *Myxotrichum uncinatum.*

MYXOTRICHUM Kunze, Myc. Hefte **2**: 108. 1823.
Actinospira Corda, Icon. Fung. **6**: 7. 1854.
Oncidium Nees (nec Swartz), Myc. Hefte **2**: 63. 1823.

Ascocarps roundish. Peridial hyphae branched, anastomosed, thick-walled, septate, smooth, or asperulate, ending partly in short spines and partly in long, septate or non-septate, rigid or flexuous, straight, curved or uncinate appendages. Asci more or less globose, 8-spored, wall evanescent. Ascospores globose, oblate or ovoid, smooth or sculptured.

TYPE species: *Myxotrichum chartarum* Kunze.

The genus *Myxotrichum* has become the collecting box for species of diverse affinities. Corda (**1854**) separated *Myxotrichum chartarum* from the other species then included in that genus, and erected the new genus *Actinospira* for it. Corda, however, considered the spores to be conidia, and placed *Actinospira* in the *Hyphomycetes.* Preuss (**1862**) also regarded the spores as conidia which were borne at the apices of the peridial prongs and appendages. The error made by these authors was due to the fact that the spores adhered to the peridial hyphae by a mucilaginous substance. Other authors regarded the various species of *Myxotrichum* as representing conidial stages of ascomycetous genera. Fuckel (**1870**) regarded *Myxotrichum* species as conidial stages of *Chaetomium* species, and reported that *M. chartarum* is the conidial stage of *Chaetomium fieberi,* while *M. resinae* is the conidial stage of *Chaetomium depressum.* Richon (**1889**) believed *M. chartarum* was the conidial stage of *Cephalotheca sulfurea* Fuckel, and he described other myxotrichums as representing conidial stages of other species of *Cephalotheca.* Boulanger (**1897**) stated that *Chaetomium chartarum* Winter has a conidial stage which was formerly called *M. chartarum.* However, he made no attempt to prove his thesis by culture work. Fries (**1832**) thought *M. chartarum* was the conidial stage of *Chaetomium chartarum.*

Costantin (**1891**) showed that *M. chartarum* and *M. aeruginosum* were ascomycetes belonging to the Gymnoascaceae. He was of the

opinion that Corda's genus *Actinospira* should be retained for *M. chartarum.* However, *Myxotrichum* is the oldest valid name and must be retained. Nees (**1823**) published the initial description of *M. chartarum,* placing it in a new genus as *Oncidium chartarum.* However, Kunze (**1823**) soon published a correction of Nees's work, since the generic name *Oncidium* already had been applied to a genus of orchids by Swartz. It was for this reason that Kunze applied the new generic name *Myxotrichum* to this species; he also described a new species of the genus, *M. murorum,* at this time.

Costantin (**1891**) stated that there were two groups of species in *Myxotrichum* which are entirely unrelated. These groups are 1) *M. chartarum,* and *M. aeruginosum,* and 2) *M. rarum, M. murorum, M. fuscum,* and *M. resinae.* He reported that species of the second group were conidial forms of ascomycetes, while the 2 species in the first group were perfect stages.

Saccardo (**1892**) divided the genus *Myxotrichum* into two genera, *Myxotrichum* Kunze for the ascigerous forms, and *Myxotrichella* Saccardo, to include the conidial forms. Included in the latter genus were *M. spelaea* (Sacc.) Sacc., the type, *M. murorum* (Kunze) Sacc., and *M. rara* (Fries) Sacc. Lindau (**1906**) followed the example of Saccardo, and placed several additional conidial types in *Myxotrichella.* These were *M. glauca* (Preuss) Lindau, *M. fusca* (Schum.) Lindau and *M. cancellata* (Phill.) Lindau.

Ferro (**1907**) examined the specimens of *Myxotrichum* which were deposited in the herbarium of Saccardo. From his observations he concluded that there were only two valid species of *Myxotrichum, M. chartarum,* and *M. ochraceum.* However, his illustration of *M. ochraceum* shows that it was *M. aeruginosum* with which he worked, and so viewed in this light, his work confirms that of Costantin, who also concluded that *M. aeruginosum* and *M. chartarum* were the only valid species of the genus. Ferro agreed with Saccardo that *Myxotrichum spelaeum* should be regarded as a *Myxotrichella* since it was only a conidial type. However, Ferro also concluded that *Myxotrichum deflexum* is an imperfect form and should be regarded as a *Myxotrichella.* Since his illustration indicates he was working with a specimen of *Myxotrichum* (*Eidamella*) *deflexum,* it is evident that he merely overlooked the ascigerous condition of this ascomycete. Ferro also stated that *Myxotrichum coprogenum* in reality represented *Gymnoascus reessii,* and in this he is supported by Massee and Salmon (**1902**). Ferro further claimed that *M. johnstoni* Massee and Salmon also represents *G. reessii,* but the illustrations and description provided by Massee and Salmon would not

support this thesis. Ferro transferred *M. folliicolum* Niessl to *Cladotrichum folliicolum* (Niessl) Ferro. He also disposed of *M. resinae* by stating that Rabenhorst's specimen (Fungi Europ. No. 2645) in Saccardo's herbarium is not *M. resinae* but *Helminthosporium resinae* Bresadola. Ferro believed *M. resinae* might better be sought under *Rhacodium resinae* Fr. The modern interpretation of *Myxotrichum* can be traced to Schroeter (**1893**), Matruchot and Dassonville (**1901**), Fischer (**1897**) and Lindau (**1906**), who agreed in considering the genus *Myxotrichum* as a representative of the Gymnoascaceae, with *M. chartarum* as the type species.

KEY TO THE SPECIES OF MYXOTRICHUM

A. Appendages septate .... B
AA. Appendages unicellular, septa lacking .... E
B. Appendages uncinate C
BB. Appendages straight or nearly so, not uncinate .... D
C. Appendages enlarged apically; ascocarps 150–350 μ diam.; cultures white, lacking red shades .... 1. *M. chartarum*
CC. Appendages uniform, not apically enlarged; ascocarps smaller than *M. chartarum;* cultures showing an admixture of red .... 2. *M. carminoparum*
D. Ascocarps dark-brown to black; peridial hyphae smooth; appendages straight or partially curved apically .... 3. *M. aeruginosum*
DD. Ascocarps ocher-brown; peridial hyphae asperulate; appendages always straight .... 4. *M. spinosum*
E. Ascospores smooth, rarely minutely asperulate and if so then appendages short, 75–353 μ, and always uncinate .... F
EE. Ascospores asperulate or echinulate; appendages usually not uncinate, but if so, long, 252–542 μ .... G
F. Ascocarps large, 300–795 μ diam., yellow, red-brown or orange-brown; appendages rigid, uncinate, 75–353 μ long; ascospores usually smooth, rarely minutely asperulous .... 5. *M. uncinatum*
FF. Ascocarps small, 90–120 μ diam., yellow to yellow-green; appendages flexuous, not curved or uncinate apically; ascospores smooth .... 6. *M. johnstoni*
G. Colonies white, vegetative hyphae hyaline; reverse colorless to yellowish; appendages usually hooked or inrolled apically; initials consist of two similar gametangia .... 7. *M. thaxteri*
GG. Vegetative hyphae red-orange or yellow-orange; reverse red-orange; appendages usually straight or curved apically, less frequently hooked .... H
H. Ascospores ovoid and globose, if globose 2.1–2.8 μ diam.; appendages 302–644 μ long; antheridium slender, ascogonium central and club-like .... 8. *M. emmonsii*
HH. Ascospores ovoid and globose, if globose 2.8–3.1 μ diam.; appendages 226–731 μ long; gametangia similar, short, club-like, apically apposed .... 9. *M. conjugatum*

1. M. CHARTARUM (Nees) Kunze, Myc. Hefte **2**: 110. 1823.
   Oncidium chartarum Nees, Myc. Hefte **2**: 63. 1823.
   Actinospira chartarum (Nees) Corda, Icones Fung. **6**: 7. 1854.
   Conoplea atra Pers., Syn. Meth. Fung., 235. 1801; Myc. Eur. **1**: 12. 1822.
   Dematium olivaceum Schum., Enum. Plant. Saell. **2**: 445. 1803.
   Stilbospora chartarum Ehrenb., Syl. Myc. Berol. 21. 1818.
   Sporotrichum chartaceum Pers., Myc. Eur. **1**: 83. 1822.
   Oidium chartarum Link, Linn. Spec. Pl. 4 ed. **6**(1): 124. 1824.

Cleistothecia globose, about 150–500 μ diam., not including the appendages, brown-black to black. Peridial hyphae branched, anastomosed, smooth, thick-walled, septate, dark black-brown, 1.7–3.3 μ diam., ending in numerous, short, spine-like thorns, and in less numerous, elongate, uncinate appendages, 50–175 μ long, smooth, 6–9 septate, 2.4–3.3 μ diam. at the base, 4.5–6.0 μ near the apex. Asci ellipsoid, hyaline, 5–7 × 6–8 μ, 8-spored, evanescent. Ascospores orange-brown, ovoid, 2.4–2.6 × 4.3–5.2 μ, finely striate with longitudinal furrows. Chlamydospores clavate, doliform or oblong, intercalary or terminal, solitary or in chains, 1.3–3.3 × 3.2–8.0 μ.

TYPE LOCALITY: Germany.

HABITAT: Paper, cardboard, straw, rotting wood, decaying leather, grouse dung, soil.

DISTRIBUTION: Germany, U.S.S.R., Italy, France, Switzerland, England, Maine, Massachusetts.

ILLUSTRATIONS: Benjamin, Aliso **3**, *pl. 8, f. 1–5;* Kunze, Myc. Hefte **2**, *f. 1;* Cooke, Handb. of Brit. Fungi **2**: 612, *f. 281;* Corda, Icon. Fung. **6**, *pl. 2, f. 23;* Costantin, Mucédinées Simples, *f. 137;* Ferro, Nuov. Giorn. Bot. Ital. II. **14**, *pl. 3, f. 1;* Fischer, E. and P. Nat. Pflanzenf. **1**(1): 296, *f. 211G;* Church, Ann. Mag. Nat. Hist. III. **9**, *pl. 6;* Preuss, Sturm Deutschl. Flora Part 3, **6**, *f. 40, A–D;* Clements and Shear, Gen. Fung., *pl. 6, f. 6.*

The above description is based on that presented by Benjamin (**1956**). The description given by Sée (**1919**) is very similar. Schroeter (**1893**), Nannizzi (**1926**), and Costantin (**1891**) present somewhat different measurements, but this can be attributed to strain variation.

2. M. CARMINOPARUM Robak, Nytt Mag. Naturvidenskab. **71**: 201. 1932.

Ascocarp greenish, 150–225 μ diam., not including appendages. Peridial hyphae septate, branched, black to dark-brown. Appendages septate, dark-brown to black, 7–8 celled, uniform in diam. from base to

apex, 2–3 μ diam. and 150–160 μ long. Central mass of asci yellowish, 80–115 μ diam., average diam. 102 μ. Asci hyaline, globular-broad ellipsoid, or reversed ovoid, 6–7 × 7 μ diam., on stipes 1 μ diam. Asci ephemeral, 8-spored. Ascospores smooth, whitish-yellow, 4.5 × 2 μ. Colonies white-yellow, reverse red on wort agar. Veg. hyphae 1.2 μ diam. Chlamydospores cylindrical, unicellular, hyaline, 3.5 × 1.8–2.0 μ, in rows with adjacent spores separated by a sterile segment.

TYPE LOCALITY: Norway.

HABITAT: Wood pulp.

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Robak, Nytt Mag. Naturvidenskab. **71**: *f. 1–3.*

The above description is taken from the original.

3. M. AERUGINOSUM Montagne, Ann. Sci. Nat. Bot. II. **6**: 30. 1836.
Myxotrichum ochraceum Berk. and Br., Ann. Mag. Nat. Hist. IV. **15**: 37. 1875 (in part).

Cleistothecia dark-brown to black, spherical, 250–400 μ diam. not including appendages. Peridial hyphae branched, anastomosed, dark-brown to black, smooth, thick-walled, 2.0–3.3 μ diam., ending partly in short spines and partly in long appendages. Appendages rigid, elongate, often tapering to a very slender apical portion, usually completely straight but often partially curved apically, dark-brown to black, 6–10-septate, 250–500 μ long, 3.3 μ wide near the base. Asci globose, hyaline, 8-spored, wall evanescent, 5.5 μ diam. Ascospores elliptical, hyaline, smooth, 2.0 × 3.3–4.0 μ. Chains of oidia present.

TYPE LOCALITY: Paris, France.

HABITAT: In damp cellar, rotting wood, rope, straw.

DISTRIBUTION: England, France, Italy.

ILLUSTRATIONS: Massee and Salmon, Ann. Bot. **16**, *pl. 5, f. 76–79;* Peyronel, Ann. Mycol. **12**: 467, *f. 3, 2–7;* Ferro, Nuov. Giorn. Bot. Ital. II. **14**, *pl. 3, f. 2.*

The above description is taken from observations made by the writer on material from exsiccati of the New York Botanical Garden Herbarium. Exsiccati examined: Rabenhorst, Fungi europaei, No. 1863 (as *M. ochraceum* Berk. and Br.); Saccardo, Mycotheca italica, No. 192 (as *M. ochraceum* Berk. and Br.); Roumeguère, Fungi selecti, No. 7366 (as *M. deflexum* Berk.). Peyronel (**1914**) also recognized that *M. aeruginosum* was represented by specimens No. 1863 of Rabenhorst's Fungi europaei and No. 192 of Saccardo's Mycotheca italica. According to Massee and Salmon (**1902**) *M. ochraceum* in part belongs in *M. aeruginosum,* since many of the specimens in Berkeley's her-

barium labelled *M. ochraceum* are in actuality *M. aeruginosum,* while, as the writer mentioned in the discussion of *Eidamella deflexa* (Kuehn, **1958**), the type specimen of *M. ochraceum* in Berkeley's herbarium is actually *Eidamella* (*Myxotrichum*) *deflexa.* Ferro (**1907**) examined the specimens of *Myxotrichum* in Saccardo's herbarium, and stated that *M. ochraceum* represents a typical specimen of the genus. However, his illustration of *M. ochraceum* actually depicts *M. aeruginosum,* which indicates he was working with specimens of the latter species. Montagne (**1836**) stressed that *M. aeruginosum* was distinguished by the green or yellow-green color. This color seems to result from the vegetative hyphae and not from the ascocarp, since in the exsiccati of Rabenhorst the mycelium was yellow-green.

4. M. SPINOSUM Massee and Salmon, Ann. Bot. **16**: 64. 1902.

Cleistothecia ocher-brown, spherical, up to 1 mm diam. Peridial hyphae minutely asperulate, brown, outermost hyphae strongly arched and bearing long, smooth, rigid, always completely straight, black-brown, septate, seta-like appendages. Asci globose, 6 μ diam., 8-spored. Ascospores ellipsoid, smooth, hyaline, 2.0 × 3.0 μ.

TYPE LOCALITY: England.

HABITAT: Dead branches of *Fraxinus,* oak bark, pineapple pericarp.

DISTRIBUTION: England, Iowa.

ILLUSTRATIONS: Massee and Salmon, Ann. Bot. **16**, *pl. 4, f. 63–66;* Gilman et al., Iowa Acad. Sci. Proc. **64**: 90, *f. 6.*

The above description is based on those given by Massee and Salmon (**1902**) and Saccardo (**18**: 195. 1906). Massee's original drawings now in the herbarium of the New York Botanical Garden were examined. On the sheet were written as synonyms *Gymnoascus caltrop* Renny and *Myxotrichum caltrop* Renny. According to Massee and Salmon, Renny collected the type specimens and deposited them in Berkeley's herbarium at Kew. Possibly Renny made his own determinations prior to the valid description published by Massee and Salmon.

5. M. UNCINATUM (Eidam) Schroeter, Cohn Krypt.-Fl. Schles. **3**(2): 212. 1893.

Gymnoascus uncinatus Eidam, Cohn Beitr. Biol. Pfl. **3**: 292. 1880.

Cleistothecia red-brown, yellowish or orange-red, globose, 300–795 μ diam., including appendages. Peridial hyphae forming a network, thick-walled, septate, asperulate, yellow-brown to orange shades, with few short spine-like ends, and with many elongate, uncinate, non-septate,

smooth appendages. Appendages variable in length in different strains, 75–353 μ, light-brown. Asci hyaline, obovate to globose, 6.7–7.2 × 8.4–9.8 μ, 8-spored, wall evanescent. Ascospores hyaline to pale orange-brown, smooth, oblate, globose or ellipsoid, variable in different strains, from 2.8–5.5 μ diam. Chlamydospores present, terminal or intercalary, asperulate, hyaline. Racquet mycelium present.

TYPE LOCALITY: Germany.

HABITAT: Bones in hen house, dung of sparrow, mouse, goat, hen, dog.

DISTRIBUTION: Germany, England, Illinois, Connecticut, Massachusetts.

ILLUSTRATIONS: Kuehn, Mycologia **47**, *f. 1–17, 35;* Benjamin, Aliso **3**, *pl. 9, f. 1–6;* Eidam, Cohn Beitr. Biol. Pfl. **3**, *pl. 14, f. 34, pl. 15, f. 39–43;* Massee and Salmon, Ann. Bot. **15**, *pl. 17, f. 30–32;* Fischer, E. and P. Nat. Pflanzenfam. **1**, *f. 211, H–K;* Clements and Shear, Gen. Fung. *pl. 6, f. 5.*

The above description is adapted from those of Kuehn (**1955**a), Benjamin (**1956**), Schroeter (**1893**), Eidam (**1880**) and Massee and Salmon (**1901**). There appears to be much strain variation in this species.

6. M. JOHNSTONI Massee and Salmon, Ann. Bot. **16**: 64. 1902.

Cleistothecia subglobose, 90–120 μ diam., at first yellow, then yellow-green. Peridial hyphae reticulate, irregularly branched, septate, 5–6 μ diam., ending partly in free ends, simple or forked as in *G. reessii,* and partly in elongate appendages, flexuous, apically visibly attenuated but not curved or uncinate. Asci subglobose, 8–9 μ diam., 8-spored. Ascospores hyaline, smooth, oblate, 3.5–4.5 × 2 μ.

TYPE LOCALITY: Gold Coast, Africa.

HABITAT: Rat dung.

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Massee and Salmon, Ann. Bot. **16**, *pl. 5, f. 113–118.*

This description is based on that of Massee and Salmon (**1902**). Massee's original drawing of this species, now included in the herbarium of the New York Botanical Garden, was examined. On the sheet was written as a synonym *Myxotrichum chlorinum,* M. and S. Ferro (**1907**) in his review of the genus as represented in Saccardo's herbarium stated that *M. johnstoni* actually represented *Gymnoascus reessii.* One explanation for Ferro's conclusion is that the long appendages were broken off from the specimens in question, leaving only the shorter free ends which Massee and Salmon state are similar to those of *G. reessii.*

7. M. THAXTERI Kuehn, Mycologia **47**: 878. 1955.

Cleistothecia spherical, light-brown to brown, 214–479 μ diam. not including the appendages. Peridial hyphae light-yellow, septate, thick-walled, asperulate, ending partly in short, asperulate spines and partly in elongate appendages. Appendages all hooked or inrolled apically, smooth, non-septate, 2.7–3.3 × 252–542 μ. Asci hyaline, elliptical to obovate, 5–5.6 × 6.8–7.2 μ, 8-spored, wall evanescent. Ascospores hyaline, echinulate, globose and 2.8–2.9 μ diam., or ovoid and 2.6–2.7 × 2.7–2.8 μ. Vegetative hyphae hyaline. Racquet mycelium present. Oidia hyaline, 1.4–1.6 × 2.8–7.2 μ.

TYPE LOCALITY: Haiti.

HABITAT: Dung of opossum-shrew (*Solenodon*).

DISTRIBUTION: Known only from the type collection.

ILLUSTRATIONS: Kuehn, Mycologia **47**, *f. 1–22, 60.*

This description is based on the original.

8. M. EMMONSII Kuehn, Mycologia **47**: 539. 1955.

Cleistothecia spherical, 189–418 μ diam., exclusive of the appendages, light to dark-brown. Peridial hyphae light-yellow, asperulate, septate, thick-walled, 2.6–3.0 μ diam., ending partly in short, asperulate spines and partly in elongate appendages. Appendages non-septate, often straight, but sometimes loosely or incompletely hooked apically, smooth, 2.8–4.2 × 302–644 μ. Asci hyaline, oval to subglobose, 5.2–5.6 × 6.5–7.0 μ, 8-spored, wall evanescent. Ascospores hyaline, echinulate, globose and 2.1–2.8 μ diam., or ovoid and 2.1–2.6 × 2.8–3.2 μ. Vegetative hyphae yellow-orange. Racquet mycelium present. Oidia hyaline, 1.4 × 2.6–7.0 μ.

TYPE LOCALITY: Georgia.

HABITAT: Bat and dog dung.

DISTRIBUTION: Georgia; Cambridge, Massachusetts; Israel.

ILLUSTRATIONS: Kuehn, Mycologia **47**: 883. 1955.

The above description is adapted from the original. A specimen in the herbarium of the National Fungus Collections, Beltsville, Md., also represents *M. emmonsii.* It is labeled *Gymnoascus* sp., collected by *G. H. Martin, No. 688,* April 23, 1917.

9. M. CONJUGATUM Kuehn, Mycologia **47**: 883. 1955.

Cleistothecia spherical, 252–504 μ diam., excluding the appendages, light to dark-brown. Peridial hyphae light-yellow, asperulate, septate, thick-walled, 2.6–3.0 μ diam., ending partly in short, asperulate spines and partly in elongate appendages. Appendages non-septate, smooth,

straight or curved apically, 2.8–3.2 × 226–731 μ. Asci hyaline, elliptical to obovate, 4.2–5.0 × 6.8–7.1 μ, 8-spored, wall evanescent. Ascospores hyaline, spherical, delicately asperulate, and measuring 2.8–3.1 μ diam. or ovoid and 2.6 × 2.9–3.2 μ. Vegetative hyphae orange. Racquet mycelium present. Oidia hyaline, 1.2–1.5 × 4.0–4.4 μ.

TYPE LOCALITY: Arizona.

HABITAT: Soil.

DISTRIBUTION: Known only from the type locality.

ILLUSTRATIONS: Kuehn, Mycologia **47**, *f. 23–41, 61.*

This description is taken from the original.

10. M. BRUNNEUM Rostrup, Bot. Tidsskr. **19**: 206. 1895.

The descriptions given by Rostrup (**1895a**) and Saccardo (**1895**) are too inadequate to permit placement of this species in the key. However, it is evident that this species is ascigerous, since the "conidia" are described as clumped, as if they had arisen from an ascus. The description is as follows: Ascocarps globose, brown, 0.5 mm diam. Hyphae loose and anastomosing, brown, septate, 3.5 μ diam., thick-walled, rough. Conidia globose, yellow-brown, pallid, 3–4 μ diam., often 8 in clumps. Habitat: On larva of acorn borer infected with *Isaria,* Copenhagen, Denmark.

EXCLUDED SPECIES

Saccardo lists 24 species of *Myxotrichum,* many of them known only from their original descriptions, which often were fragmentary. This genus became the collecting box for unrelated types. Saccardo (**1892**) divided the genus into two genera, *Myxotrichum* Kunze, to include the ascigerous forms, and *Myxotrichella* Saccardo, to include the conidial types. *Myxotrichum spelaeum* was designated as the type for the new genus *Myxotrichella,* which included three species, *M. spelaea, M. murorum,* and *M. rara.*

MYXOTRICHUM SPELAEUM Saccardo, Michelia **2**: 554. 1881 = *Myxotrichella spelaea* Sacc., Syll. Fung. **10**: 593. 1892.

This species is described as a conidial form only. Ferro (**1907**) agreed with Saccardo that this species should be considered to represent *Myxotrichella.*

M. MURORUM Kunze, Myc. Hefte **2**: 110. 1823 = *Myxotrichella murorum* (Kunze) Sacc., Syll. Fung. **10**: 593. 1892.

This is another of the species known only as conidial forms.

M. RARUM Fries, Syst. Myc. **3**: 347. 1832 = *Myxotrichella rara* (Fr.) Sacc., Syll. Fung. **10**: 593. 1892.

Fries (**1832**) and Saccardo (**4**: 320. 1886) list *Conoplea hispidula* Alb. and Schw., nec Pers., as a synonym for this species. Corda (Icon. Fung. **6**, 1854) states that *M. rarum* shows "true excipula of the family Phragmotrichaceae" (Melanconiales). This species is described as a conidial type.

M. CANCELLATUM Phillips, Grevillea **13**: 51. 1884 = *Myxotrichella cancellata* (Phill.) Lindau, Krypt. Fl. Deutsch. **8**: 714. 1906.

This species is described as a conidial form. However, the hyphae surrounding the spore mass are described by Phillips as being similar to "*M. ochracea* Berk. and Br."

M. CAESIUM Fries, Syst. Myc. **3**: 348. 1832.

Corda, in Icon. Fung. **2**, and Saccardo (**4**: 329. 1886) place this species in synonymy with *Gonytrichum caesium* Nees. It is known as a conidial form only.

M. AURANTIACUM (Peck) Saccardo, Syll. Fung. **4**: 319. 1886.
Gymnascella aurantiaca Peck, Jour. Myc. **1**: 57. 1885.
Gymnoascus aurantiacus (Peck) Sacc., Syll. Fung. **8**: 823. 1889.

A discussion of the placement of this species is found in the section on excluded species of *Gymnoascus,* under *G. aurantiacus.*

M. COPROGENUM Saccardo, Michelia **2**: 372. 1881 = *Gymnoascus reessii* Baranetzky.

A discussion of the synonymy of this species is presented in the section on *G. reessii.*

M. COPROGENUM var. MALACENSE Sacc. and Paoletti, Myc. Malac. n. 120, and Sacc. Syll. Fung. **10**: 593. 1892 = *Gymnoascus reessii* Baranetzky.

The synonymy of this species is discussed under *G. reessii.*

M. DEFLEXUM Berk., Ann. Mag. Nat. Hist. **1**: 260. 1838 = *Eidamella deflexa* (Berk.) R. K. Benjamin.

For a discussion of this species see the section on *E. deflexa* (Kuehn, **1958**).

M. FOLIICOLUM Niessl (Hedwigia **17**: 176. 1878, nom. nud.) ex Sacc., Syll. **4**: 319. 1886 = *Cladotrichum foliicolum* (Niessl) Ferro, Nuov. Giorn. Bot. Ital. II. **14**: 228. 1907.

This fungus is described as a conidial type. The writer has examined the specimen in the exsiccati of Rabenhorst, Fungi europaei, No. 2465, and found no gymnoascaceous fungus present. Saccardo (**4**: 319. 1886) states "perhaps it is a state of *Meliola* or *Campsotrichum.*" Ferro (**1907**) examined that specimen in Saccardo's herbarium and concluded that it represented a new species of *Cladotrichum.*

M. FUSCUM (Schumacher) Fries, Syst. Myc. **3**: 349. 1832.
Dematium fuscum Schum., Enum. Plant. Saell. **2**: 444. 1803.
Myxotrichella fusca (Schum.) Lindau, Krypt. Fl. Deutschl. **8**: 714. 1906.

According to Corda, Icon. Fung. **6**, this species actually represents a pathological or senile form of *Chaetomium.*

M. GLAUCUM Preuss, Linnaea **25**: 74. 1852.
Myxotrichella glauca (Preuss) Lindau, Krypt. Fl. Deutschl. **8**: 714. 1906.

This species is described only as a conidial type.

M. MOLLE Fries, Syst. Myc. **3**: 348. 1832.

Corda, in Icon. Fung. **6**, states that this fungus is a species of *Botrytis.* It is described as being a conidial type.

M. OCHRACEUM Berkeley and Broome, Ann. Mag. Nat. Hist. IV. **15**: 37. 1875; Cooke, Grevillea **3**: 184. 1874.

Massee and Salmon (**1902**) state that the type specimens in Berkeley's herbarium in reality represent *Eidamella deflexa,* while other specimens sent out by Berkeley proved to represent *M. aeruginosum.* Ferro (**1907**) examined the specimens of *M. ochraceum* in Saccardo's herbarium and concluded that this species and *M. chartarum* represent typical species of *Myxotrichum.* However, his illustrations of *M. ochraceum* show that it was *M. aeruginosum* with which he was working. Peyronel (**1914**) examined several exsiccati specimens (see under *M. aeruginosum*) supposedly *M. ochraceum,* but which actually represented *M. aeruginousm.* He concluded that *M. ochraceum* is not a

distinct species, but should be considered to be a mixture of 2 different species. From these reports, it can be concluded that *M. ochraceum* in part represent *Eidamella deflexa*, and in part is *M. aeruginosum*.

M. PATULUM Fries, Syst. Myc. **3**: 350. 1832.

Corda, in Icon. Fung. **6**, states that this fungus is a pathological or senile form of *Chaetomium*.

M. SIMILE Berkeley and Curtis, Grevillea **3**: 146. 1874.

This fungus was discovered on a culm of *Arundinaria* in South Carolina and is described as bearing terminal heads of conidia in chains. In the exsiccati of Berkeley and Curtis, North American Fungi, No. 1388, which the writer obtained from the New York Botanical Garden, there is a specimen labeled *Myxotrichum affine* B. and C. which is also on a culm of *Arundinaria* from South Carolina. The label on the outside of the packet is *M. affine*. The writer has been unable to locate a published description of, or reference to, *M. affine*, and it is possible that *M. affine* and *M. simile* represent the same fungus. At any rate, the specimen in the exsiccati mentioned above did not contain a gymnoascaceous fungus.

M. MURINUM Fries, Syst. Myc. **3**: 350. 1832.

Fries gives this further information: *Botrytis murina* Dittm. apud Sturm, l.c. Heft **3**, *t. 36;* Pers. Myc. **1**: 61; Link, Linn. Spec. Pl. 4 ed. **6**(1): 61. Corda, in Icon. Fung. **6**, also places *M. murinum* as a species of *Botrytis*.

M. UNICOLOR Fries, Syst. Myc. **3**: 351. 1832.
Campsotrichum unicolor Ehrenb., Hor. Phys. Ber. 83. 1820.

Corda, in Icon. Fung. **6**, places this species as a representative of *Campsotrichum*.

M. BICOLOR Fries, Syst. Myc. **3**: 351. 1832.
Campsotrichum bicolor Ehrenb., Hor. Phys. Ber. 32. 1820, and Link's Jahrb. Gewachsk. II. **1**: 32. 1819.

Corda, Icon. Fung. **6**, states that this fungus is a species of *Campsotrichum*.

M. RESINAE Fries, Syst. Myc. **3**: 349. 1832.

This species is a conidial type, and is placed by Fries and by Saccardo (**4**: 320. 1886) in synonymy with *Rhacodium aterrinum* Ehrenb. Corda, in Icon. Fung. **6**, transferred this species to *Dendryphium* Wallroth., as *D. resinae*. The writer examined the specimen in Karsten's exsiccati, Finland Fungi, and found no gymnoascaceous fungus present. Ferro (**1907**) examined the specimen in Rabenhorst's exsiccati, Fungi europaei, No. 2645, which was present in Saccardo's herbarium, and stated that it was not *M. resinae* Fries, as labeled, but more properly represented *Helminthosporium resinae* Bresadola.

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BIBLIOGRAPHY

Bakhtin, V. S. 1928. Fungi which damage books. Proc. Pan Soviet Congr. Bot. Leningrad **1928**: 169–170.

Baranetzky, J. 1872. Entwicklungsgeschichte des *Gymnoascus reessii*. Bot. Zeit. **30**: 145–160.

Benjamin, C. R. 1955. Ascocarps of *Aspergillus* and *Penicillium*. Mycologia **47**: 669–687.

Benjamin, R. K. 1956. A new genus of Gymnoascaceae with a review of the other genera. Aliso **3**: 301–328.

Berkeley, M. J. 1838. Notices of British fungi. Ann. Nat. Hist. **1**: 257–264.

——. 1874. Notices of North American fungi. Grevillea **3**: 145–160.

——, **and C. E. Broome.** 1875. Notices of British fungi II. Ann. Mag. Nat. Hist. IV. **15**: 28–41.

Bisby, G. R., N. James, and M. Timonin. 1933. Fungi isolated from Manitoba soil by the plate method. Can. Jour. Res. C. **8**: 253–275.

Blumer, S. 1945. Bodenpilze aus dem Schieferschutthalden von Engi (Glarus). Mitteil. Naturf. Ges. Kantons Glarus **7**: 185–203.

Bodin, E. 1907. Sur un nouveau champignon du favus (*Achorion gypseum*). Ann. Derm. Syph. **8**: 585–602.

Boudier, E. 1892. Description de deux nouvelles espèces de *Gymnoascus* de France. Bull. Soc. Myc. Fr. **8**: 43–45.

Boulanger, E. 1897. Sur une forme conidienne nouvelle dans le genre *Chaetomium*. Rev. Gén. Bot. **9**: 17–26.

Brefeld, O. 1891. Untersuchungen aus dem Gesamtgebiete der Mykologie **10**: 158–160.

Cain, R. F. 1957. Studies of coprophilous Ascomycetes VI. Species from the Hudson Bay area. Can. Jour. Bot. **35**: 255–268.

Church, A. H. 1862. Note on *Myxotrichum chartarum* (Kunze). Ann. Mag. Nat. Hist. III. **9**: 32–33.

Clements, F. C., and C. L. Shear. 1931. The genera of fungi. H. W. Wilson, New York. i–iv, 496 pp.

Cocconi, G. 1891. Osservazione e ricerche sulla sviluppo di tre piccoli funghi. Mem. R. Accad. Sci. Bologna V. **2**: 27–36.

Cooke, M. C. 1871. Handbook of British fungi. 2 vols., Macmillan, New York. 981 pp.

——. 1874. British fungi. Grevillea **3**: 177–186.

Conard, A. 1940a. Sur l'ascocarpie et la forme conidienne de *Gymnoascus reessii* Baran. poussant sur le bois. Bull. Soc. Bot. Belg. **72**: 75–91.

——. 1940b. Sur la toupie d'enroulement de *Gymnoascus reessii*. Bull. Soc. Biol. **133**: 670.

——. 1940–1941. Sur *Coniophora cerebella* et sur les champignons qui se sont associés à lui dans un cas de destruction de planchers. Bull. Soc. R. Belg. **72**: 93–116.

Corda, A. C. J. 1837–1854. Icones fungorum. 6 vols. J. G. Calve, Prague.

Costantin, J. 1888. Les mucédinées simples. P. Klincksieck, Paris. 210 pp.

——. 1891. Note sur le genre *Myxotrichum*. Bull. Soc. Bot. Fr. **38**: 344–348.

Dale, E. 1903. Observations on Gymnoascaceae. Ann. Bot. **17**: 151–196.

DeLamater, E. D. 1937. *Eidamella spinosa* (Matruchot and Dassonville) refound. Mycologia **29**: 572–582.

Dodge, C. W. 1935. Medical mycology. Mosby, St. Louis. 900 pp.

Ehrenberg C. G. 1818. Sylvae mycologicae berolinensis. Bruschke, Berolini. 32 pp.

——. 1819. Fungi nova genera tria. Link's Jahrb. der Gewachskunde II, **1**: 32.

——. 1820. Horae physicae berolinensis. Bonn.

Eidam, E. 1880. Beiträge zur kenntnis der Gymnoascaceen. Cohn Beitr. Biol. Pfl. **3**: 267–305.

——. 1882. Über Entwicklungsgeschichte der Ascomyceten. Bot. Centr. **10**: 106–107.

Emmons, C. W. 1931. Observations on *Achorion gypseum*. Mycologia **23**: 87–95.

——. 1954. Isolation of *Myxotrichum* and *Gymnoascus* from the lungs of animals. Mycologia **46**: 334–338.

Ferro, G. 1907. Osservazioni critiche antorno ad alcune specie conservate nell'erbario micologico P. A. Saccardo riferite al gen. *Myxotrichum* Kunze. Nuov. Gior. Bot. Ital. II. **14**: 221–234.

Fischer, A. 1897. Engler and Prantl, Die naturl. Pflanzenfam. **I**(1): 294.

Fries, E. M. 1832. Systema mycologicum **3**: 346–351.

Fuckel, L. 1870. Symbolae mycologicae. Jahrb. Nassau. Ver. Naturk. **23–24**: 1–459.

Gilman, J. C. 1957. A manual of soil fungi. 2 ed. Iowa State College Press, Ames, Iowa. I–XIV, 450 pp.

——, **L. H. Tiffany, and R. W. Lichtwardt.** 1957. Fungi new to Iowa. Iowa Acad. Sci. Proc. **64**: 85–92.

Gola, G. 1930. L'erbario micologico di P. A. Saccardo. E. Antoniana, Padova. 329 pp.

Grigorakis, L. 1929. Dermatophytes et dermatomycoses. Ann. Derm. Syph. VI. **10**(1): 18–68.

Hennings, P. 1903. Einige deutsche Dung bewohnende Ascomyceten. Hedwigia **42** (Beibl.): 181–185.

Kellerman, W. A. 1885. New literature. Jour. Myc. **1**: 56–58.

Klocker, A. 1902a. *Gymnoascus flavus* n. sp. Hedwigia **41**: 80–83.

——. 1902b. *Gymnoascus flavus* n. sp. Bot. Cent. **89**: 626.

——. 1902c. *Gymnoascus flavus* n. sp. Bot. Tidsskr. **25**: 49–52.

——. 1903. *Gymnoascus flavus* n. sp. Rev. de Myc. **25**: 43–44.

Kuehn, H. H. 1955a. Observations on Gymnoascaceae. I. *Myxotrichum uncinatum* and a new species of *Myxotrichum*. Mycologia **47**: 533–545.

——. 1955b. Observations on Gymnoascaceae. II. Two new species of *Myxotrichum*. Mycologia **47**: 878–890.

——. 1956. Observations on Gymnoascaceae. III. Developmental morphology of *Gymnoascus reessii*, a new species of *Gymnoascus* and *Eidamella deflexa*. Mycologia **48**: 805–820.

——. 1958. A preliminary survey of the Gymnoascaceae. I. Mycologia **50**: 417–439.

Kunze, G. 1823. Einige neue oder verkannten Pilzgattungen und Arten. X. *Myxotrichum*. Myk. Hefte **2**: 108–110.

Lagarde, J. 1913. Champignons (première série). Arch. Zool. Expér. et Génér. **53**: 277–307.

Lind, J. 1910. Systematic list of Fungi (Micromycetes) from north-east Greenland. Medd. Greenland **43**: 149–162.

Lindau, G. 1906. Die Pilze. Fungi Imperfecti. Rabenhorsts Kryptogamen-Flora von Deutschland **8**: 714–716.

——. 1905. Kryptogamen-Flora der Mark Brandenburg **7**: 74.

Lindfors, T. 1920. Einige bemerkenswerte, aus Kulturerde isolierte Pilze. Svensk Bot. Tidskr. **14**: 267–276.

Lodhi, S. A., and A. Naeem. 1955. Some seed-borne fungi from Pakistan. Brit. Myc. Soc. Trans. **38**: 240–242.

Luerrsen, C. 1879. Handbuch der systematischen Botanik, mit besonderer Berucksichtigung der Arzneipflanzen. H. Hassel, Leipzig. 2 vols.

Malan, C. E. 1949. Su un nuovo reperto di *Dicyma ambigua* Peyronel e sulla posizione sistematica di questa species. Nuov. Gior. Bot. Ital. II. **56**: 735–738.

Massee, G. 1895. British fungus flora IV. George Bell and Sons, London. 522 pp.

——, **and E. S. Salmon.** 1901. Researches on coprophilous fungi. Ann. Bot. **15**: 313–358.

—— **and** ——. 1902. Researches on coprophilous fungi. II. Ann. Bot. **16**: 57–93.

Matruchot, L., and C. Dassonville. 1901. *Eidamella spinosa*, dermatophyte préduisant des périthèces. Bull. Soc. Myc. Fr. **17**: 123–132.

Montagne, C. 1836. Cryptogames nouvelles de la France. Ann. Sci. Nat. Bot. II. **6**: 28–36.

Morini, F. 1889. Ricerche sopra una nuova Gimnoascea. Mem. R. Accad. Sci. Bologna IV. **10**: 201–208.

Nannizzi, A. 1926. Ricerche sui rapporti morfologici e biologici tra Gymnoascaceae e Dermatomiceti. Ann. Myc. **24**: 85–129.

——. 1927. Ricerche sull'origin saprofitica dei funghi delle tigne. II. *Gymnoascus gypseum* (n. sp.), forme ascophora del *Sabouraudites* (*Achorion*) *gypseum* (Bodin) Ota et Langeron. Atti R. Accad. Fis. Siena X. **2**: 89–97.

Nees von Esenbeck, T. F. L. 1823. Fungorum novorum pemptas. Myk. Hefte **2**: 61–66.

Ota, M., and M. Langeron. 1923. Nouvelle classification des dermatophytes. Ann. Parasitol. Hum. Comp. **1**: 305–336.

Peck, C. H. 1884. Report of the Botanist. Rep. N. Y. St. Mus. Nat. Hist. **35**: 125–164.

Persoon, C. H. 1801. Synopsis methodica Fungorum. Dieterich, Gottingae. Parts 1 and 2, 706 pp.

——. 1822–1828. Mycologia europaea. Erlangiae. **1**. 1822, **2**. 1825, **3**. 1828.

Peyronel, B. 1914. Osservazioni critiche e sperimentali su alcune specie del genere *Dicyma* Boul. et sui loro stati ascofori. Ann. Myc. **12**: 459–470.

Phillips, W., and C. Plowright. 1884. New and rare British fungi. Grevillea **13**: 48–54.

Preuss, C. G. T. 1852. Übersicht untersuchter Pilze, besonders aus der Umgebung von Hoyerswerda. Linnaea **25**: 71–80.

——. 1852. Literarische Gegenbemerkung. Bot. Zeit. **10**: 501–503.

——. 1862. Sturm's Deutsch. Fl. part 3, **6**: 79–80.

Rabenhorst, L. 1878. Fungi europaei exsiccati Cent. 25. Hedwigia **17**: 171–176.

Raper, K. B., and C. Thom. 1949. A Manual of the Penicillia. Williams and Wilkins, Baltimore. i–x, 875 pp.

Rayss, T., and S. Borut. 1958. Contribution to the knowledge of soil fungi in Israel. Mycopath. Mycol. Appl. **10**: 142–174.

Richon, C. 1889. Description de deux espèces nouvelles du genre *Cephalotheca* Fuckel. Bull. Soc. Myc. Fr. **5**: 105–111.

Robak, H. 1932. Investigations regarding fungi on Norwegian ground wood pulp and fungal infection at wood pulp mills. Nyt Mag. Naturvidenskab. **71**: 185–330.

Rostrup, E. 1894. Oest-Groenlands Svampe. Medd. om Groenland **18**: 1–39.

——. 1895a. Mykologiske meddelelser V. Bot. Tidsskr. **19**: 201–214.

——. 1895b. Contributions mycologiques V pour le année 1893. Bot. Tidsskr. **19**: 215–218.

——. 1897. Mykologiske meddelelser VII. Bot. Tidsskr. **21**: 37–49.

Saccardo, P. A. 1881a. Fungi veneti. Michelia **2**: 241–301.

——. 1881b. Fungi aliquot extra europaei. Michelia **2**: 372–376.

——. 1882. Fungi veneti novi vel critici vel Mycologiae Venetae addendi. Michelia **2**: 528–563.

——. Sylloge Fungorum. P. A. Saccardo, Pavia, Italy. 1886. **4**: 317–320; 1889. **8**: 823–824; 1892. **10**: 71, 593; 1895. **11**: 437–438, 615; 1899. **14**: 824; 1902. **16**: 805; 1906. **18**: 195–196; 1928. **24**(2): 1145–1146.

Sartory, A., and G. Bainier. 1913a. Études morphologique et biologique d'un champignon nouveau de genre *Gymnoascus*, *Gymnoascus confluens*, n. sp. Bull. Soc. Myc. Fr. **29**: 261–272.

—— **and** ——.1913b. Étude d'un champignon nouveau de genre *Gymnoascus*, *Gymnoascus confluens* n. sp. Compt. Rend. Soc. Biol. **74**: 498–500.

Schroeter, J. 1893. Die Pilze Schlesiens. In Cohn Krypt.-Fl. Schles. **3**(2): 210–213.

Schumacher, C. F. 1803. Enumerato plantarum Saellandiae. F. Brummer, Hafniae. 489 pp.

Sée, P. 1919. Les maladies du papier piqué. O. Doin and Fils, Paris. 168 pp., 17 pls.

Smith, A. L. 1896a. Fungi new to Britain. Brit. Myc. Soc. Trans. **1**: 150–158.

——. 1896b. The fungi of germinating farm seeds. Brit. Myc. Soc. Trans. **1**: 182–186.

——. 1900. Some new microscopic fungi. Jour. R. Micr. Soc. **1900**: 422–424.

——, **and J. Ramsbottom.** 1917. New or rare microfungi. Brit. Myc. Soc. Trans. **5**: 422–433.

——, **and C. Rea.** 1902. Fungi new to Britain. Brit. Myc. Soc. Trans. **2**: 31–40.

Stoppel, R. 1907. *Eremascus fertilis*, nov. spec. Flora **97**: 332–346.

Tate, P. 1929. The dermatophytes or ringworm fungi. Biol. Rev. **4**: 41–75.

Vailionis, L. 1936. Une nouvelle espèce de *Gymnoascus*. Vyt. Didziojo Univ. Mat. Gamtos Fak. Darbai **11**: 115–121.

Wallroth, F. G. 1833. Flora cryptogamica Germaniae. J. L. Schragii, Norembergae. Vol. 2, lvi, 923 pp.

Warcup, J. N. 1950. The soil plate method for isolation of fungi from soil. Nature **166**: 117–118.

——. 1951. Studies on the growth of Basidiomycetes in soil. Ann. Bot. II. **15**: 305–317.

Winter, G. 1887. In Rabenhorst Krypt.-Fl. Deutsch. **1**(2): 2, 3, 15–17.

Zukal, H. 1887. Über einige neue Ascomyceten. Verhandl. Zool.-Bot. Ges. Wien **37**: 39–46.

——. 1889. Entwickelungsgeschichtliche Untersuchungen aus dem Gebiete der Ascomyceten. Akad. Wiss. Wien, Math.-Nat. Kl. Sitzber. Abt. 1, **98**: 520–603.

——. 1890. Über einige neue Pilzformen und über das Verhaltniss der Gymnoascen zu den ubrigen Ascomyceten. Ber. Deutsch. Bot. Ges. **8**: 295–303.

STAGES OF DEVELOPMENT IN RHIZOMORPHIC THALLI OF ARMILLARIA MELLEA [1]

PHILIP J. SNIDER [2]

(WITH 5 FIGURES)

Rhizomorphs and mycelial strands occur widely in the Ascomycetes, Basidiomycetes, and Fungi Imperfecti, but yet the structure, development, and functions of these common vegetative organs have not been studied intensively. At the present time there appears to be no obvious morphological distinction between a mycelial strand and a rhizomorph, for these structures exist in a continuum from simple to complex, some being little more than individual hyphae or aggregations of hyphae, as in *Ophiobolus graminis,* and others ranging upward to highly elaborate rhizomorphs containing well organized apices and differentiated cell-types, as in *Sphaerostilbe repens, Merulius lacrimans,* and *Armillaria mellea.* From the most complex to the simplest, rhizomorphs and strands are found in saprophytes, like *M. lacrimans, Agaricus campestris,* and parasites, like *Armillaria mellea, Corticium* (= *Rhizoctonia*) *solani.*

Reviews of the comparative morphology (Garrett, **1944**) and ecology (Garrett, **1951**, **1956**) of various strand- and rhizomorph-producing fungi have shown that the parasitic species form an ecologically specialized but taxonomically unrelated group of root-inhabiting fungi. The strands and rhizomorphs of existing species have been arranged in a morphological series suggesting the emergent steps that may have occurred in the evolution of the most elaborate types, although such steps possibly arose independently and followed somewhat different courses in the several unrelated taxonomic groups. Much research of fundamental importance remains to be done in the comparative study of strands and rhizomorphs, as is indicated by recent contributions from Macdonald

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(**1949**), Garrett (**1954**), and Townsend (**1954**), but the work to be reported here and in several subsequent papers is limited to experiments upon rhizomorph development in the one species *Armillaria mellea.*

Rhizomorphs have an important function in the life cycle of this fungus. Primarily, *Armillaria mellea* is a facultative parasite of roots in a wide variety of woody, perennial plants throughout the forested areas of the world. The rhizomorphs provide a method for vegetative propagation, the only natural means of asexual reproduction known for this species. Growth of rhizomorphs is also the most common method the fungus uses to extend itself from host to host. Basidiospores are probably responsible for occasionally transporting the fungus to widely separated, uninfected locales, although at present this is unproven; its likelihood is suggested because fruiting occurs abundantly in nature and because the copiously produced basidiospores germinate readily in pure culture. Saprophytism is limited in nature to substrates which die after becoming infected, as this specialized root parasite is generally unable to colonize dead substrates in competition with soil-inhabiting fungi. The pseudosclerotium, a structure enclosing portions of infected host tissue within a thin, crusty envelope of melanin, is thought to enable the fungus to endure periods of unfavorable biological competition with secondary invaders of vigorous saprophytic character; the rhizomorph, somewhat analagous to the asexual spores of most parasitic fungi, extends the fungus rapidly but locally in space when conditions favor the conquest of new hosts. These and other aspects of the general biology of *Armillaria mellea* are reviewed in detail elsewhere (Snider, **1957**).

In this and subsequent papers the term *mycelium* will be restricted to the hyphal mycelium exclusive of rhizomorphs; the word *thallus* will be used when referring to a mycelium and its attached rhizomorphs inclusively. Such usage is a departure from that of previous authors, who have often left the reader unable to decide whether rhizomorphs were or were not included in what the author called "mycelium." In addition to avoiding this possibility of confusion, distinguishing mycelium from rhizomorphs may also help to emphasize certain basic differences between the two. The chief architectural feature of a mycelium, a branching system of hyphae with substrate between the individual hyphae, is expressly inapplicable to the rhizomorph of *A. mellea,* which has no substrate between the individual files of cells within it. The fringe of laterally directed hyphae often surrounding the rhizomorph is more accurately described as mycelium derived from the rhizomorph, as root hairs are derived from roots, than as part of the rhizomorph proper. In volume for volume of space occupied, rhizomorphs expose

much less surface area to the substrate than do mycelia. This difference in surface to volume ratio, an important consequence of the difference in cellular organization, immediately suggests the possibility of dissimilarities in function as well.

There are two morphological types of rhizomorphs in *A. mellea.* The darkly pigmented, round type, once known as *Rhizomorpha subterranea,* and the almost white, usually lighter-pigmented, flat type, once known as *R. subcorticalis,* are most often seen in nature in the habitats suggested by these archaic binomials. Since it can be easily shown that the two types are not simply a response to the environment (either form can be produced in the absence of soil or of plant parts), the old terms are abandoned even for descriptive purposes by this author; the two types will be referred to simply and unassumingly as *round* or *flat* rhizomorphs.

Hartig (**1873**) showed that both *Rhizomorpha subterranea* and *R. subcorticalis* Persoon were vegetative structures belonging to the same species as the then separately known fruit-body *Agaricus melleus* Vahl (**1790**) ex Fries (**1821**), a synonym of *Armillaria mellea* (Vahl ex Fr.) Quélet (**1872**). Brefeld (**1877**), in confirming Hartig's discovery, isolated *single* basidiospores from freshly collected mushrooms supplied by Hartig and demonstrated that a single spore, isolated in pure culture, grew into a mycelium which produced the same type of rhizomorph found attached to the fruit-body from which the spore had been isolated. Brefeld's work is historically important in two respects: it was one of the first instances of pure culture technique with *any* organism (contemporary with Koch's famous work, **1877**), and it was the first careful description of the initiation and apical growth of rhizomorphs, based upon microscopic observations. Some important contributions, to be cited later, have been added to this early work during the past 80 years, but, as Brefeld's researches have not been widely read, many authors have unknowingly and needlessly done little more than confirm Brefeld's results. The present work, then, is the continuation of a line of research having its historic inception in 1875, the actual time of Brefeld's experiments.

MATERIALS AND METHODS

Most of the living material used in this work was isolated as single basidiospores from freshly collected fruit-bodies. Each monosporous isolate will be identified by a fraction: the numerator is the stock number, or basidiocarp parent; the denominator is the mycelial strain number, or individual basidiospore. Strain 3/6, for example, originated from the sixth basidiospore isolated from the third fruit-body.

Stock 1, the only stock not derived directly from basidiospores, originated as an air contaminant in a tobacco callus-tissue culture in the laboratory of Dr. Katharine Tryon at Wellesley College. Inasmuch as the callus had been in pure culture for two years and *A. mellea* is not known to produce asexual spores, the chance inoculum must have been an airborne basidiospore. Stock 1 consists of 24 strains derived vegetatively from the original isolate in a special study of somatic variation, the results of which will be published at a later date. The original isolate was identified as *A. mellea* in the keys to cultural characteristics devised by Davidson et al. (**1942**) and Nobles (**1948**), and the identification was verified by F. F. Lombard of the United States Department of Agriculture and Prof. S. D. Garrett of Cambridge University.

The stocks in which spores were isolated from fresh fruit-bodies were as follows: stock 2, 16 isolates, Lincoln, Mass.; stock 3, 6 isolates, Lincoln, Mass.; stock 4, 39 isolates, Lincoln, Mass.; stock 5, 11 isolates, Waltham, Mass.; stock 6, 6 isolates, Lincoln, Mass.; stock 7, 14 isolates, Lincoln, Mass.; stock 8, 21 isolates, Barett, New Hampshire; and stock 9, 115 isolates, Barett, N. H. The fruit-bodies were identified in the keys and descriptions of Fries (**1821**) and Quélet (**1872**) and in several current manuals, and the identifications were verified by checking the characteristics of the isolated progeny in the keys for vegetative characters of Davidson et al. (**1942**) and Nobles (**1948**).

The basidiospores were germinated and isolated in the following manner: an excised gill was suspended over a petri dish of fresh potato-glucose agar for a few minutes, the resulting spore-fall was streaked evenly over the whole dish, and then the spores were incubated at room temperature in subdued light. Better than 90 per cent of the spores germinated within one to three days, and germlings were isolated with a small, chisel-edged, sewing needle under a dissecting microscope at about 30 diameters magnification.

The culture medium was fresh potato-extract, glucose agar used at a measured volume of 30 ml in each petri dish of 10 cm diameter. The medium was prepared in the usual way by combining a boiling-water extract of 200 g fresh weight of Irish potato with 20 g of glucose and 20 g of Difco Bacto Agar to make 1 liter of medium. The final pH, after autoclaving and cooling to room temperature, was 6.5 to 7.0.

Benton and Ehrlich (**1941**) claim, without supporting data, that the rhizomorphs of *A. mellea* have a sharp optimum for growth at pH 5.0, but this requirement is evidently not as critical as these authors supposed. The rhizomorphs used in this laboratory grow abundantly on various media from pH values of about 4.0 to 7.0. Difco Potato-Dextrose Agar,

for example, which has a pH of 5.5 after autoclaving, gives no better growth of rhizomorphs than does the fresh medium described above. (The Difco product will give much less growth, in fact, unless about 100 μg of thiamin, an essential growth factor for *A. mellea*, is added per liter of medium, as the Difco product is not nearly as rich in thiamin as fresh potato extract.) The abundant growth on the fresh medium, incidentally, is specifically not brought about by the pH being shifted from 7.0 to 5.0 during growth, as few strains of *A. mellea* will change the pH as much as one full unit during six weeks growth on this (Snider, unpublished data) or other ordinary media (Reitsma, **1932**). Although Reitsma found the optimum to have a plateau from pH 4.5 to 6.5 for the growth of "mycelium" (Reitsma did not indicate whether or not rhizomorphs were included), there are apparently no equally precise data available for rhizomorphs; however, their response is probably similar to that of the mycelium.

Inoculum consisted of 1-mm cubes of agar, cut from the fringe of actively growing thalli; the exact age of the thalli was considered unimportant so long as the mycelium was in its linear phase of radial growth rate. All portions of rhizomorphs and their rudiments were carefully excluded from the inoculum. Each petri dish was inoculated with a single cube, placed at the center of the dish. Pouring of plates and inoculating of cultures were done in a highly aseptic chamber equipped with U.V. germicidal lamps. Such unusual precautions were important for two reasons. *A. mellea* is a slow-growing fungus, usually requiring about four weeks to complete growth in a petri dish, and it seldom grows well in competition with other fungi. As a result of the aseptic precautions, the loss through contamination rarely exceeded one per cent of the cultures.

The cultures were incubated at a constant temperature of 25° C in total darkness. The temperature selected is in the narrow optimal plateau for the response of rhizomorph growth to temperature (Bliss, **1946**; Townsend, **1954**; Snider, **1957**), and light was excluded because there is some evidence that relatively bright white light inhibits the growth of rhizomorphs (Raabe, **1953**, abstract; Townsend, **1954**; Snider, **1957**). All observations were made under illumination from a deep red safe-light of a type to which orthochromatic photographic emulsions are insensitive. The cultures were also protected from loss of moisture either by sealing them with Scotch brand drafting tape, which gives adequate protection for about 6 weeks, or by enclosing them in closely fitting cardboard boxes holding 12 plates each, which worked efficiently for about 4 weeks. The boxes were much less troublesome than the

tape when large numbers of plates were involved and also provided a convenient safeguard against accidental exposure to white light.

STAGES OF DEVELOPMENT

A generalized scheme for the development of the thallus in a typical rhizomorphic strain of *A. mellea* will be described as observable in a petri-dish culture incubated under the conditions outlined in Materials and Methods. The generalization is based upon the study of growth in the laboratory of many isolates from a number of sources. The sequence of events in plate culture may be divided into five meaningful and easily recognizable stages based upon gross anatomical landmarks of the process, and, although these five stages will serve as useful focal points for the description, they are not intended to obscure the important realization that development is actually continuous, surpassing most presumptuous attempts to fit its dynamic features into static categories.

During the first week of growth only mycelium is apparent. This is as true of thalli begun from single basidiospores as of those begun from mycelial inoculum. The growth of this *central mycelium* (as opposed to the lateral mycelium described later) preliminary to the plainly visible emergence of rhizomorph "initials" (see below) will be called *stage 1* of development. The microscopic induction and inception of the "initials," it should be understood, occur somewhat before the end of stage 1 as defined. Stage 1 is thus the pre-emergent stage for a rhizomorphic thallus. The microscopic beginnings of initiation are difficult to see in the dense center of an agar-plate culture and were not studied in detail for this reason, but Brefeld (**1877**) believed that he successfully traced the origin in his liquid cultures to either a single hypha or several closely associated hyphal branches that begin to undergo rapid cell division and hyphal branching with a minimum of cell elongation. The cells hypertrophy somewhat, become irregularly shaped, and fuse into a rounded, compact mass of pseudotissue. These early events, as described by Brefeld, should be re-examined under modern conditions suitable for a critical confirmation of his observations.

The surface of the dense mass of cells, or *microsclerotium,* soon becomes tinted with melanin, which is typically the first obvious sign of rhizomorph initiation. *Stage 2* of development is the relatively brief period during which the rhizomorph "initials" (see below) become plainly visible: thus stage 2 is the emergent stage of thallus development but must be regarded as rhizomorph initiation in this restricted sense only. One or more spots on each microsclerotium usually remain dis-

tinctly white after pigmentation develops, and it is at these white spots that the growing apices of rhizomorphs emerge. As the disoriented histology within the microsclerotium (Brefeld, **1877**) is quite unlike the highly polarized organization of the cells within the emerging apex, the term "initial" in the usage of recent decades evidently needs some clarification. The term has presumably been applied to both the microsclerotium and any emerging apices, but it is not at all certain that most authors have used it in this sense. The present author has chosen to specify microsclerotia and apices as such and to drop the term "initial" for the present. The microsclerotia, mostly embedded in the agar but virtually always in contact with its surface, normally form a tight cluster at the center of the young thallus. The localization of the microsclerotia at the agar surface is determined by the dependence of initiation upon the availability of air, as shown in the simple experiments described below. No further initiation normally occurs, either in this stage or later, provided the growth of the rhizomorphs from these first microsclerotia is fairly abundant; if rhizomorph growth from this first group is limited, microsclerotia will occasionally continue to emerge, distributed in markedly atypical patterns over the whole culture (Snider, **1957**). The dynamic features of stage 2 development, then, are the enlarging and pigmenting of the microsclerotia, the organizing of the rhizomorph apices within the microsclerotia, and the emerging of these apices for the first few millimeters of extension growth.

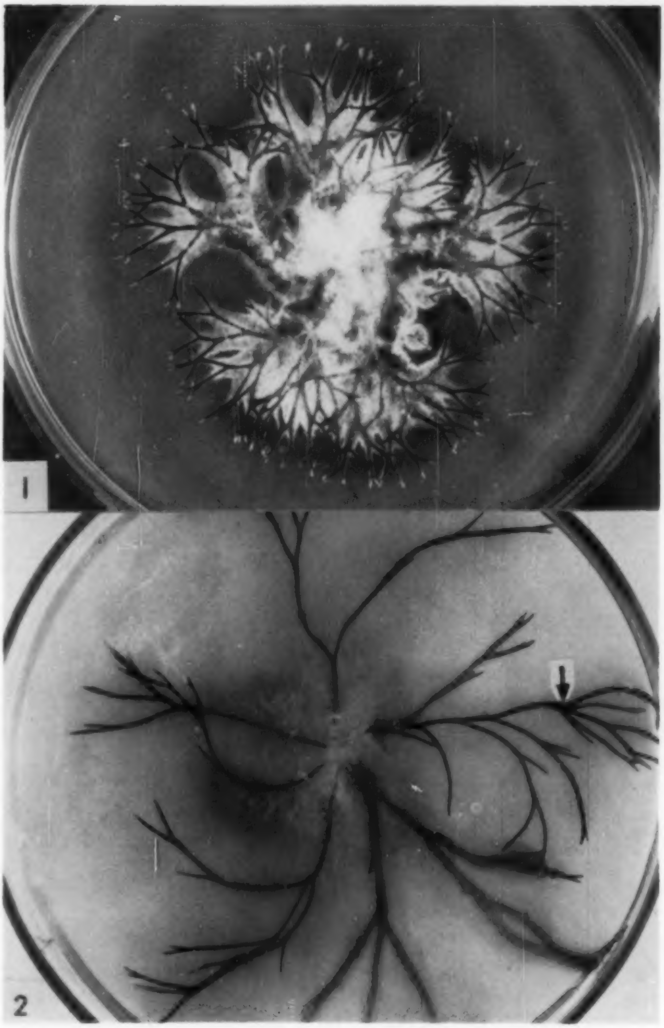
The description of the stages of thallus development will be interrupted briefly at this point, in order to include two experiments designed to account for the observation that microsclerotia never seemed to occur suspended in the aerial mycelium or submerged completely in the agar. The results indicate that this localization at the surface of the agar reflects a requirement of microsclerotial initiation for an adequate exposure to air. In one experiment hyphal fragments of strain 1/8 were stab-inoculated into 50 deep columns of fresh potato-glucose agar. In many of the tubes the desired effect occurred of several mycelia originating well separated from one another and varying from 0.5 to 12 cm below the surface. Some of the tubes produced a surface mycelium as well, but most of them did not. Invariably microsclerotia appeared solely in the surface mycelia, although even the deepest mycelia grew. All the submerged mycelia were of sufficiently thin growth to permit clear observation to the center of each, so that there was no possibility of overlooking microsclerotia. Once initiated, the rhizomorphs from the surface mycelia grew rapidly, of course, to the bottom of the tubes.

In the other experiment 1.5 liters of a very rich liquid medium, con-

taining potato extract, yeast extract, and sucrose, were autoclaved in a two liter flask and inoculated with one cube of agar containing mycelium of strain 7/6. The cube sank immediately to the bottom of the flask, and the flask was left on a table in the laboratory with no special precautions taken for controlling external conditions. The inoculum grew quite slowly from the bottom as a dome-shaped central mycelium, but showed no suggestion of rhizomorph initiation. In this instance the hemispherical shape of the mycelium allowed a clear view of the center of the mycelium through the bottom of the flask. After almost two months without initiating rhizomorphs the mycelium finally reached the surface of the liquid; whereupon, an abundance of microsclerotia emerged at the surface, and during the following month the rhizomorphs from these microsclerotia proceeded to ramify through the entire volume of liquid in an entangled mass. This mycelium, after growing two months without producing microsclerotia, was still capable of doing so, but only after gaining free access to the atmosphere.

The rhizomorph apices, newly emerged (stage *2*) at the agar-air interface in petri plates, usually grow slowly for one to several days. *Stage 3* is the period during which the rhizomorphs, although now more than several millimeters long, have not yet entered the area beyond the limits of the central mycelium. Defined in this way stage 3 will ordinarily refer to a thallus with newly initiated rhizomorphs that are in the normal lag phase of growth, but it will also include thalli with rhizomorphs that are in an abnormally slow linear phase of growth. The rhizomorphs of the latter may never outgrow the central mycelium (Snider, **1957**), so that stage 3 is the terminal stage of development for thalli of this sort. For most strains, however, stage 3 is a relatively short period during which the rate of rhizomorph growth is accelerating.

The rhizomorph of *Armillaria mellea*, even at this young stage, is no simple aggregation of vegetative hyphae. The terminal half-millimeter of this remarkably complex organ contains a compact growing point of small, approximately isodiametric cells. This meristematic zone is protected by a cap of intertwined hyphae in a slimy matrix. Behind the apex is a zone of elongation a millimeter or so in length. The middle of the rhizomorph is a hollow space occupied by a column of air that extends all the way to the base of the growing point. Adjacent to this lumen is a tissue of noticeably hypertrophied, elongated cells that undoubtedly serve for some specialized function, such as transport or storage. The diameter of these cells is four or five times that of the ordinary cells in vegetative hyphae. These large cells grade into smaller ones toward the periphery of the rhizomorph, and at the periphery there



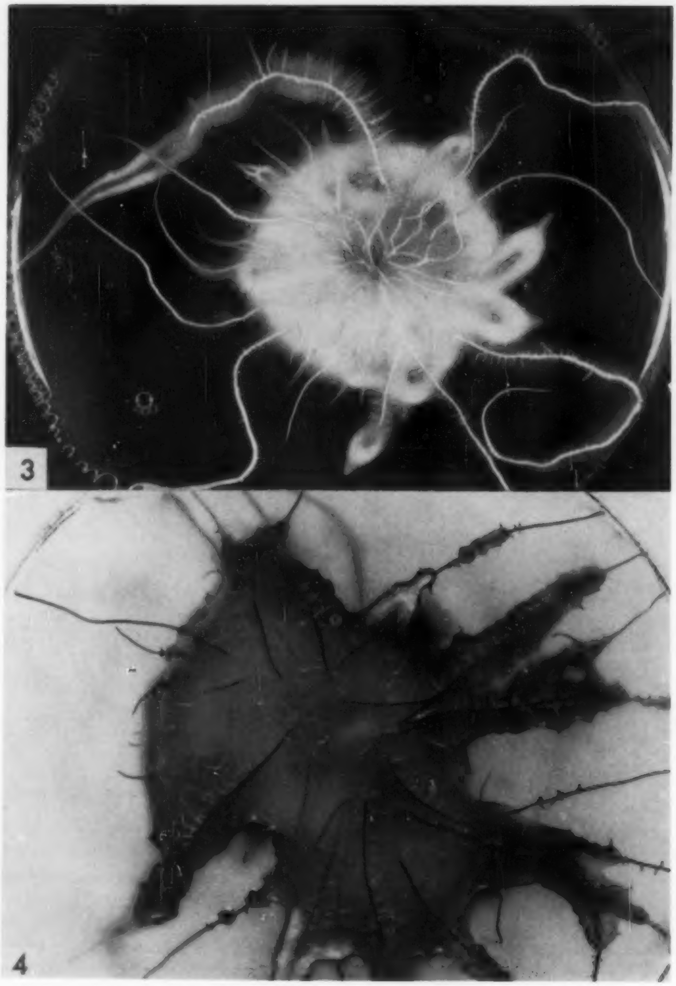
FIGS. 1–2.

Armillaria mellea. FIG. 1. Dichotomous branching strikingly exhibited by rhizomorphs in a culture of strain 7/12, which characteristically dichotomizes its rhizomorphs frequently. Top view. FIG. 2. Palmate branching (arrow) of a rhizomorph in a culture of strain 1/8. This thallus is in stage 4 of development and has round, pigmented rhizomorphs. Top view.

are several layers with thickened walls. These epidermal layers are incrusted with melanin in pigmented rhizomorphs. A rhizomorph hair zone of vegetative hyphae, analogous to the root hairs of higher plants and oriented similarly, may protrude from the epidermal layers in the mature zone of the rhizomorph. Those seeking more information about the internal anatomy of rhizomorphs must go to Brefeld (**1877**), as no detailed study comparable to this early work was found in the literature.

When the accelerating rhizomorphs reach their linear phase of apical growth rate, which exceeds the radial growth rate of the central mycelium by a factor of 5 or more, the general appearance of the thallus is entirely changed by the rhizomorphs, which thrust radially into the uninhabited substrate far ahead of the central mycelium. This is *stage 4* of thallus development, and its essential characteristic is that the rhizomorphs maintain a constant (or nearly so) and significantly faster apical growth rate than the central mycelium. During this stage the number of principal rhizomorphs is increased primarily by *dichotomous branching* of the terminal apices (FIG. 1), and although the beginnings of the hair zone and lateral branches may appear, these lateral expressions tend to be held in check as long as the terminal apices are growing rapidly. Another type of branching, in which one terminal apex divides simultaneously into more than two daughter apices, is not too common for round rhizomorphs in plate culture. It is common in liquid cultures, in nature, and in flat rhizomorphs. *Palmate branching,* as it will be called, is probably not fundamentally different from dichotomous branching and is seen in one of the rhizomorphs in FIG. 2. The *hair zone* and young *lateral branches,* a basically different type of branching, are illustrated in FIG. 3 in a thallus about to enter stage 5 development.

Apical growth of the principal rhizomorphs is indeterminate, theoretically, but after a week or more of stage 4 in the confinement of a plate culture, where the rate is slowed at the periphery, emphasis shifts from terminal to lateral development. The acutely radiate appearance of stage 4 is gradually transformed into the broadly lobed thallus of *stage 5* development. Although some lateral branches may be initiated in stage 4, as indicated above, their growth is mainly in stage 5, the stage of diminishing over-all growth in plate cultures. Stage 5 is thus the terminal stage of development. The lateral branches do not originate from the pre-existing terminal apices, as in the other methods of branching; they arise *de novo* and endogenously (de Bary, **1887**) within the mature zone of the rhizomorph, an origin curiously similar to that of secondary roots in higher plants. In plate cultures the lateral branches merely fill the interstices among the radially oriented, primary



FIGS. 3–4.

Armillaria mellea. FIG. 3. Hair zone and young lateral branches of rhizomorphs in a thallus of strain 1/6, which has nearly completed stage 4 of thallus development. This strain has round, non-pigmented rhizomorphs. Bottom view. FIG. 4. Pseudosclerotia in a thallus of strain 1/3. Several pseudosclerotia have coalesced, enveloping most of the radially oriented rhizomorphs and the central mycelium within a single, fused structure. A small, isolated pseudosclerotium is located on the rhizomorph at the one o'clock position. Bottom view.

rhizomorphs. The hair zones, having grown laterally to an appreciable extent, are now composed of branching, multicellular hyphae and will be called *lateral mycelia* in this well-developed condition. The pseudosclerotium (FIG. 4), if it appears at all, is formed late in stage 5, either as cylindrical or arched, melanin-impregnated sheaths enveloping most of the lateral mycelia, so that each rhizomorph becomes a sort of tube within a tube; or as a dome covering the central mycelium and extending below the substrate to the bottom of the dish. Several pseudosclerotia may be formed, and they often coalesce to sharply accentuate the lobed appearance of the stage 5 thallus (FIG. 4).

Stage 5 is the terminal stage for thallus development in ordinary plate

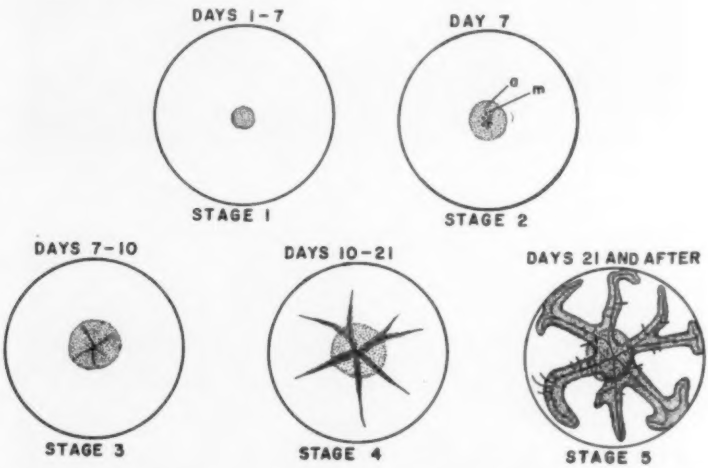


FIG. 5. Diagrammatic summary of the stages of thallus development in rhizomorph-producing strains of *Armillaria mellea*. Stage 1: Pre-emergence of rhizomorphs. Only mycelium, the central mycelium, is plainly visible. Incipient initiation of rhizomorphs occurs microscopically late in stage 1. Stage 2: Emergence of rhizomorphs. Microsclerotia (m) with emerging apices (a) become plainly visible and apical growth begins. The microsclerotia were drawn loosely clustered for the sake of clarity. Stage 3: Lag phase of rhizomorph growth. Apical growth rate of the rhizomorphs is accelerating, but the rhizomorphs have not yet grown beyond the central mycelium. Stage 4: Linear phase. The thallus is acutely radiate in over-all appearance. Rhizomorph apical growth rate is maximal and nearly constant; dichotomous branching is typical; the hair zone and the beginning of lateral branching are often evident, as shown. Stage 5: Terminal phase. Thallus broadly lobed. Radial growth stopped or retarded; lateral mycelium and lateral branches extend laterally from rhizomorphs; pseudosclerotia, not shown here (see FIG 4), may form in the mycelium; all growth diminishes.

cultures, but the formation of fruit-bodies might be considered as a further stage, if fruiting of *A. mellea* can occur in petri dishes. Fruiting was not observed in any of the cultures used in this study. The morphological stages of thallus development just described in detail are summarized diagrammatically in FIG. 5.

DISCUSSION

The stages of thallus development presented in this paper will be of most direct significance to the experimental work to be published in subsequent papers, as it is not suggested that either the exact sequence of events or the radially symmetrical thalli necessarily occur in plate cultures precisely as development occurs in nature. There are probably similarities, however, and several of these will be discussed here.

The mode of rhizomorph growth exhibited in stage 4 development in plate cultures definitely has its counterpart in nature. The rapid terminal extension of rhizomorphs, with occasional dichotomous branching and with relative inactivity of lateral development, is the means whereby the thallus extends itself through soil from host to host as well as through other regions similarly low in nutrient. Fast-growing rhizomorphs may possibly outdistance the slowly diffusing metabolic byproducts from the central mycelium that nourishes the rapidly extending apices, thus enabling the fungus to penetrate deeply into unexploited substrate.

The counterpart in nature of stage 5 development, however, is observed in the actual exploitation of fresh substrate. Such accentuated lateral development is seen in the penetration of host roots as well as in the ramification of soft, starch-laden tissues. As a rhizomorph tip touches the root of a potential host, rather than penetrating directly, it grows appressed to the surface of the root for a way and initiates a number of lateral branches; it is the lateral branches that actually penetrate the bark of the root. The mode of penetration and ramification of the host has been observed by many and studied in detail by Thomas (**1934**). Histological evidence (Kusano, **1911**; Day, **1927**; Thomas, **1934**) suggests that penetration is accomplished more through enzymatic than mechanical action.

Another basic similarity in the development of laboratory and natural thalli of *A. mellea* is undoubtedly the initiation of rhizomorphs at the substrate-air interface. This requirement for ready access to the atmosphere may be related to a special need of the organism during growth of rhizomorphic thalli. The air requirement probably indicates

a high oxygen requirement for rhizomorph initiation, although no attempt has been made yet to confirm this probability. Rhizomorph apices grow in length much faster than hyphal tips, and probably have a higher oxygen requirement per unit weight. Münch (**1909**) and Reitsma (**1932**) have shown that the oxygen for growing apices is supplied through the air canal in the middle of the rhizomorph. A high oxygen requirement for rhizomorph initiation would be an adaptive mechanism inasmuch as it would insure that wherever initiation occurred the air in the lumen of the resulting rhizomorphs will be continuous with that in the atmosphere. Whenever oxygen becomes limiting for apical growth, the thallus will be compelled to revert to the slower mycelial growth until the mycelium encounters another substrate-air interface; whereupon, it may reinitiate rhizomorphs. When growing rhizomorphs meet a new interface, they establish a new, direct connection between the lumen and the atmosphere; it is thus possible for thalli in nature to extend themselves from host to host indefinitely without necessarily initiating rhizomorphs *de novo* at each new center of growth. Consequently, the first two stages of thallus development in plate cultures may not occur very frequently in nature.

SUMMARY

The rhizomorphs of *Armillaria mellea* are grown easily in pure culture and lend themselves readily to precise experimentation as well as to classroom use. This paper contains a description of the general aspects of development in a rhizomorphic thallus and is based upon the study of many monosporous isolates from several sources. Thallus development has been divided into 5 stages (summarized in FIG. 5): pre-emergence of rhizomorphs, emergence, lag phase of rhizomorph growth, linear phase, and terminal phase. Some details of growth and anatomy are also described and illustrated. The paper is intended primarily as the foundation for several future experimental papers about specific aspects of rhizomorph development, but it will also be useful to anyone desiring to grow rhizomorphs of *A. mellea* in pure culture. This species is particularly suitable for laboratory demonstrations of growing rhizomorphs and of fungal bioluminescence, and the methods described here for isolating and culturing the fungus may be considerably simplified for such purposes.

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LITERATURE CITED

de Bary, A. 1887. Comparative Morphology and Biology of the Fungi, Mycetozoa, and Bacteria. Clarendon Press. Oxford.

Benton, V. L. and J. Ehrlich. 1941. Variation in culture of several isolates of *Armillaria mellea* from western white pine. Phytopathology **31**: 803–811.

Bliss, D. E. 1946. The relation of soil temperature to the development of *Armillaria* root rot. Phytopathology **36**: 302–318.

Brefeld, Oscar. 1877. Basidiomyceten. Botanische Untersuchungen über Schimmelpilze **3**: 136–173. Arthur Felix. Leipzig.

Davidson, R. W., W. A. Campbell, and D. E. Vaughn. 1942. Fungi causing decay of living oaks in the eastern United States and their cultural identification. U. S. D. A. Tech. Bull. 785.

Day, W. R. 1927. The parasitism of *Armillaria mellea* in relation to conifers. Quart. Jour. For. **21**: 19–21.

Fries, Elias. 1821. Systema mycologicum. Vol. I. Officina Berlingiana. Lund.

Garrett, S. D. 1944. Root disease fungi. Chronica Botanica. Waltham.

——. 1951. Ecological groups of soil fungi: a survey of substrate relationships. New Phytol. **50**: 149–166.

——. 1954. Function of the mycelial strands in substrate colonization by the cultivated mushroom, *Psalliota hortensis*. Brit. Myc. Soc. Trans. **37**: 51–57.

——. 1956. Biology of root-infecting fungi. University Press. Cambridge.

Hartig, R. 1873. Vorläufige Mitteilung über den Parasitismus von *Agaricus melleus* und dessen Rhizomorphen. Bot. Zeit. **31**: 295–297.

Koch, Robert. 1877. Untersuchungen über Bacterien. V. Die Aetiologie der Milzbrand-Krankheit, begründet auf die Entwicklungsgeschichte des Bacillus Anthracis. Cohn, Beitr. Biol. Pflanzen. **2**: 277–310.

Kunsano, S. 1911. *Gastrodia elata* and its symbiotic association with *Armillaria mellea*. Jour. Coll. Agr. Tokyo **4**: 1–66.

Macdonald, J. A. 1949. The heather rhizomorph fungus, *Marasmius androsaceus* Fries. Edinburgh Royal Soc. Proc., Sec. B. **63**: 230–241.

Münch, E. 1909. Untersuchungen über Immunität und Krankheitsempfanlichkeit der Holzpflanzen. Naturwiss. Zeitschr. Forst- Landwirtsch. **7**: 129–160.

Nobles, M. K. 1948. Studies in forest pathology. VI. Identification of cultures of wood-rotting fungi. Canadian Jour. Res. C. **26**: 281–431.

Quélet, L. 1872. Les champignons du Jura et des Vosges. Mém. Soc. Émul. Montbéliard II. **5**: 42–332.

Raabe, R. D. 1953. Cultural studies of *Armillaria mellea*. (Abstract.) Phytopathology **43**: 482.

Reitsma, J. 1932. Studien über *Armillaria mellea* (Vahl) Quél. Phytopath. Zeit. **4**: 461–522.

Snider, P. J. 1957. Rhizomorph development in *Armillaria mellea* (Vahl ex Fr.) Quél. Ph.D. Thesis. Harvard University.

Thomas, H. E. 1934. Studies on *Armillaria mellea* (Vahl) Quél., infection, parasitism, and host resistance. Jour. Agr. Res. **48**: 187–218.

Townsend, B. B. 1954. Morphology and development of fungal rhizomorphs. Brit. Myc. Soc. Trans. **37**: 222–233.

Vahl, M., ed. 1790. Flora Danica. Vol. 6. Fasc. 17, pl. 1013. Nicolai Mölleri et Filii. Copenhagen.

HETEROTHALLISM IN THE LETTUCE STRAIN OF ERYSIPHE CICHORACEARUM

W. C. Schnathorst

Very little is known about the sexuality of different species of the Erysiphaceae. Homma (**2**) found that *Sphaerotheca fuliginea* (Schlect.) Pollacci is homothallic. Yarwood (**7**) showed that *Erysiphe cichoracearum* DC. ex Mérat is heterothallic on sunflower, *Helianthus annuus* L. Studies on *Erysiphe graminis hordei* Em. Marchal and *E. graminis tritici* Em. Marchal, by Cherewick (**1**) and Powers and Moseman (**3**), indicated that these fungi are both homothallic and heterothallic.

The present study was undertaken to provide additional information on sexuality in the Erysiphaceae and to lay the groundwork for future studies on the inheritance of pathogenicity in *E. cichoracearum*.

OBSERVATIONS AND EXPERIMENTAL RESULTS

The fungus was grown in detached-leaf culture in Petri dishes—on leaves of wild lettuce, *Lactuca serriola* L., rather than cultivated lettuce, *Lactuca sativa* L., because they were more easily handled. Further, the surfaces of wild-lettuce leaves remained freer from condensation, which otherwise interfered with mildew growth and encouraged the growth of fungi that parasitized this powdery mildew.

Collections of severely mildewed leaves of wild lettuce were made in the Salinas Valley of California. The collections were taken from wild-lettuce plants because perithecia were scarce on cultivated lettuce at the time of this collection. Conidia were transferred to detached leaves from areas on collected leaves where perithecia were abundant. Conidia were transferred with an alcohol-sterilized camel's-hair brush and gently tapped over the detached leaves to release the mildew conidia. Leaves for detached-leaf culture were obtained from healthy wild-lettuce plants grown in a greenhouse that was frequently checked for contaminating mildews. The leaves were washed with distilled water, dried with an air jet, and floated on about 5 ml of distilled water in Petri dishes. The leaves were provided 300 ft-c continuous illumination (Westinghouse fluorescent lamp) and incubated at about 23° C.

Perithecial formation was evident on the detached leaves in about 7 days. Conidia were consequently taken from areas on the detached leaves where perithecia were abundant, and single-conidial isolates were established by the technique described by Schnathorst (**5**). The resulting colonies were numbered and increased on wild-lettuce leaves, and each isolate was tested for pathogenicity on cultivated lettuce, variety Great Lakes. Pathogenicity determinations were necessary because it was previously shown (**6**) that 2 strains of *E. cichoracearum* occur on wild lettuce in the Salinas Valley: the Salinas wild-lettuce strain and the cultivated-lettuce strain. The Salinas wild-lettuce strain is not pathogenic on cultivated lettuce, whereas the cultivated-lettuce strain is pathogenic to both wild and cultivated lettuce.

TABLE 1

PRODUCTION OF PERITHECIA IN ERYSIPHE CICHORACEARUM IN MATINGS OF SEVERAL MONOCONIDIAL ISOLATES

Isolates crossed[a]	Perithecia[b]	Isolates grown separately[a]	Perithecia[b]
4 × 1	+	1	−
4 × 2	−	2	−
4 × 3	−	3	−
4 × 5	+	4	−
4 × 6	+	5	−
4 × 7	−	6	−
4 × 8	+	7	−
4 × 9	+	8	−
4 × 10	−	9	−
4 × 11	+	10	−
		11	−

[a] Numbers refer to the number of the isolate.
[b] + designates that perithecia were formed; − designates that they were not.

All 11 of the single-conidial isolates obtained were pathogenic on cultivated lettuce, and were designated as clones of the cultivated-lettuce strain of *E. cichoracearum*.

To determine whether the lettuce strain of *E. cichoracearum* was composed of + and − mating types, the following experiment was performed. One of the clones (No. 4) was crossed with the other 10 clones. All of the isolates were grown separately as controls. The results of this experiment (TABLE 1) indicate that 2 mating types are present. Six of the 10 matings resulted in the formation of perithecia. No perithecia developed when each isolate was grown separately. Although the population of conidia sampled was small, the results indicate that the 2 mating types occur with about the same frequency.

From these results it should follow that, if all the isolates were

crossed in all possible combinations, perithecia should form only when opposite mating types are mated.

In such an experiment, the formation of perithecia was expected to occur from 30 of the crosses. Actually, 21 of the 30 crosses with isolates of opposite mating types yielded perithecia. A check of the cultures where perithecia were expected but not observed revealed that mildew growth was scant and that colonies did not intermingle, thus offering an explanation for the failures. No perithecia resulted when isolates of the same mating type were crossed.

In additional tests perithecia formed as easily on cultivated-lettuce leaves as on wild-lettuce leaves.

The opportunity to cross different strains of *E. cichoracearum* arose during the course of this study. A strain of mildew occurs on wild lettuce in the Davis area of California that is different from the Salinas wild-lettuce and cultivated-lettuce strains. It was concluded from a previous study on the strain occurring in the Davis area (**6**) that it is the one commonly found on *Zinnia elegans* Jacq. A monoconidial isolate was obtained and tested for pathogenicity on several plant species. It was pathogenic on wild lettuce and *Z. elegans,* but not on cultivated lettuce. Since its mating type was not known, it was crossed with 3 isolates of the lettuce strain that belonged to the + mating type (arbitrarily designated), and with 3 of the − mating type. Perithecia (normal in all respects) formed only when the isolates designated + (Nos. 3, 4, and 7) were mated with it. It is thus apparent that interstrain crosses are possible.

DISCUSSION

The results of this investigation confirm those of Yarwood (**7**) in that both studies lead to the conclusion that *E. cichoracearum* is heterothallic. It therefore appears that, in the Erysiphaceae, there are species that are homothallic (*Sphaerotheca fuliginea*), some that are heterothallic (*Erysiphe cichoracearum*), and possibly some that are both homothallic and heterothallic (*E. graminis*). The latter case appears to need clarification, since the most recent work on *E. graminis* (**3**) gives no indication that this species is homothallic.

The present study offers an alternative mechanism by which the cultivated-lettuce strain of mildew may have originated. It was recently proposed by Schnathorst (**6**) that the cultivated-lettuce strain arose from the Salinas wild-lettuce strain through mutation. It was suggested that the mutation occurred on wild lettuce or on some other natural host of this strain of mildew, or on hybrid 41858 (a hybrid of wild and cultivated lettuce), which was grown in the Salinas Valley in 1940.

There is evidence that this hybrid was susceptible to the Salinas wild-lettuce strain (**6**). With evidence of heterothallism in the lettuce strain and related strains now at hand, the possibility exists that 2 different strains of mildew may have mated on a common host, the result being the recombination of genes and the recent occurrence of the lettuce strain (placed at about 1950).

It has been shown that the perithecial stage is largely necessary for survival of the lettuce strain in the Salinas Valley (**4**). It is probable that this new strain, in order to survive, had to go through the perfect stage shortly after its appearance in the Salinas Valley. If the lettuce strain did result from mutation, it is unlikely that the same mutation for pathogenicity occurred twice and that each mutant was of the opposite mating type, a condition necessary for the formation of the perfect stage. The original mutant may therefore have had to mate with the opposite mating type of another strain of mildew on a common host in order to go through the sexual cycle. The present study shows that this would have been possible.

SUMMARY

The cultivated-lettuce strain of *Erysiphe cichoracearum* was found to be heterothallic. The two mating types occurred with about the same frequency when random samples of single conidia were analyzed for their mating reaction. It was found that interstrain crosses within the species *E. cichoracearum* are possible, which may allow for recombination of genes and the formation of new mildew strains.

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LITERATURE CITED

1. **Cherewick, W. J.** 1944. Studies on the biology of *Erysiphe graminis* DC. Can. Jour. Res. C. **22**: 52–86.
2. **Homma, Y.** 1933. Homothallism in *Sphaerotheca fuliginea* (Schlect.) Pollacci. Proc. Imp. Acad. (Tokyo) **9**: 186–187.
3. **Powers, H. R., Jr., and J. G. Moseman.** 1956. Heterothallism in *Erysiphe graminis tritici* (Abstr.). Phytopathology **46**: 23.
4. **Schnathorst, W. C.** 1957. Etiology of lettuce powdery mildew (*Erysiphe cichoracearum* DC. ex Mérat). Ph.D. Thesis, Univ. of Calif.
5. ——. 1958. An efficient method of obtaining single-conidial isolates of powdery mildew. Phytopathology **48**: 390.
6. ——, **R. G. Grogan, and R. Bardin.** 1958. Distribution, host range, and origin of lettuce powdery mildew. Phytopathology **48**: 538–543.
7. **Yarwood, C. E.** 1935. Heterothallism of sunflower powdery mildew. Science II. **82**: 417–418.

EVIDENCE AGAINST FUSARIUM POAE AND SITEROPTES GRAMINUM AS CAUSAL AGENTS OF SILVER TOP OF GRASSES [1]

JOHN R. HARDISON [2]

ABSTRACT

HARDISON, J. R. (Oregon Agric. Exp. Sta., Corvallis) **Evidence against Fusarium poae and Siteroptes graminum as causal agents of silver top of grasses.** Mycologia **51**: 712-728. 1961.—Silver top, the premature death of inflorescences from damage to the lower part of the terminal or penultimate internode of grasses, was formerly considered a disease caused by *Fusarium poae* (Pk.) Wr. in association with a mite-vector *Siteroptes graminum* (Reut.). This theory is challenged by a weak association of microorganisms determined by recovery from 2355 silver-top-affected culms of *Festuca arundinacea* Schreb., *F. rubra* var. *commutata* Gaud. and *Poa pratensis* L. The exterior of the leaf sheath was surface-disinfected in 1957 but not in 1958. Nearly half of the plated stem segments remained sterile on PDA. More sterile stems were noted in collections early in the season than later, suggesting gradual invasion of dead stems by saprophytes. *S. graminum* was not recovered from more than 95% of the grass stems studied. *Fusarium poae* is easily isolated but was recovered from only 2.1% of 236 damaged stems of *F. arundinacea*, 2.9% of 102 *F. rubra* var. *commutata* stems collected in a late-pastured field, and less than 20% of all grass stems studied. The incidence of *F. poae* increased as the season advanced, suggesting progressive invasion of stems killed by other agents. Newly killed stems generally had lower incidences of *F. poae* and *S. graminum* than older dead stems with white panicles. The general absence of microorganisms in most silver-top-affected culms of grasses in Oregon, a re-valuation of the literature, and control of the disorder by DDT are interpreted as strong evidence against *F. poae* and *S. graminum* as causal agents of a disease and suggest a return to insects as the primary agents causing silver top of grasses.

Silver top, the premature death of the inflorescence resulting from an injury to the lower part of the terminal or penultimate internode, affects many grasses throughout the world. Destruction of the entire inflores-

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cence seriously reduces yield of seeds. Silver top first became widespread in Oregon during 1955 and destroyed at least half of the Chewings fescue (*Festuca rubra* var. *commutata* Gaud.) seed crop in Clackamas county and caused a loss estimated at $300,000. Studies on the problem were necessitated by this outbreak in the center of a large area devoted to production of seeds of many susceptible grasses.

Silver top is commonly believed to be a disease of grasses caused by *Fusarium poae* (Pk.) Wr. in association with mites, *Siteroptes graminum* (Reut.), as summarized by Leach (**21**). Discrepancies were noted between this explanation and results of preliminary studies in Oregon during 1953 through 1956. Therefore, studies were expanded in 1957 and 1958 to determine the association of microorganisms in the etiology of silver top.

LITERATURE REVIEW

The term silver top apparently originated in North America and was in general use in the 1880's. The first adequate description of the disorder is usually credited to Comstock (**4**). Severe damage to grasses from silver top has been reported in the United States: all New England areas (**11**), New York (**38**), Pennsylvania (**18**), Iowa (**22, 24**), Wisconsin (**35**), Rhode Island (**18**), and Oregon (**7**); southern Canada (**10**); Europe: France (**23**), Germany (**16, 32**), Spain (**1**), Finland (**14, 33**), and Russia (**27**).

The extent of possible damage is evident from the following selected locations and per cent infestations: Massachusetts, 95 per cent in *Festuca ovina* L., and *F. ovina* var. *duriuscula* (L.) Koch, 75 per cent in *Poa pratensis* L., and 85 per cent in *P. nemoralis* L. (**11**); Pennsylvania, 10 to 85 per cent in species of *Agrostis, Festuca* and *Poa* (**18**); and Wisconsin, 90 per cent in species of *Festuca* and *Poa* (**35**). Many grasses are susceptible to silver top including species of *Agropyron, Agrostis, Anthoxanthum, Arrhenatherum, Avena, Bromus, Dactylis, Deschampsia, Elymus, Festuca, Lolium, Panicum, Phalaris, Phleum, Secale, Setaria, Stipa,* and *Triticum*. However, certain grasses consistently appear to be more severely affected, particularly *Festuca arundinacea* Schreb., *F. elatior* L., *F. ovina, F. ovina* var. *duriuscula, F. rubra* L., *F. rubra* var. *commutata, Poa nemoralis,* and *P. pratensis* (**7, 8, 11, 12, 18, 33, 35, 38**).

The stem injury that results in silver top has been illustrated by Hinds (**11**), Stewart and Hodgkiss (**38**), Keil (**18**), and Scholl (**35**). Their figures agree with the first descriptions by Comstock (**5**) and Osborn (**24**) and thus establish a somewhat restricted definition. White

ear in European literature can be the same as the American silver top, but white ear also has included numerous other kinds of plant injury causing dead inflorescences.

A concensus of literature reports in the United States and Canada would define silver top as: (1) death of the entire inflorescence without apparent damage to the leaf sheath and blade borne at the node above which injury occurs, (2) restriction of the zone of injury to internode tissue above the terminal or penultimate node, (3) injury consisting of a withering of stem tissue without conspicuous wounds at one or several spots usually in close proximity, (4) remainder of culm below the injury remaining green and healthy, (5) injured internode tissue occurring with or without association of microorganisms, and (6) prevention of the disorder by DDT or related insecticides applied coincidently with emergence of inflorescences.

Thrips, *Anaphothrips obscurus* (Müll.), cause silver top in northeastern United States (**4**, **5**, **11**, **26**) and Canada (**10**), and thrips may cause white ear in Finland (**14**). Evidence against thrips is reported from Iowa (**24**, **26**), Pennsylvania (**18**), and Wisconsin (**35**). In Europe various species of thrips were implicated as causing part of the injury resulting in white ear (**16**, **32**, **42**).

Insects other than thrips have been suggested as responsible in Iowa (**24**, **26**), and other midwestern states (**39**). Unidentified insects caged on grasses did not produce silver top in Canada according to Osborn (**24**), and *Leptopterna dolabratus* (L.) was exonerated as the cause of silver top in Kentucky (**15**), Maryland (**25**), and Wisconsin (**35**). In Europe various insects are reported to be associated with white ear (**16**, **31**, **32**, **34**, **42**).

The mite *Siteroptes graminum* (Reut.) collected on affected grass stems in Finland was described in 1900 (**33**). According to Stewart and Hodgkiss (**38**), Reuter (**33**) believed that *S. graminum* was the chief agent responsible for silver top, and he described lacerations of the stem tissues that result in death of the inflorescences. The biology and taxonomy of *S. graminum* were recently reviewed (**2**, **3**). Both *S. graminum* and *Tarsonemus* spp. were associated with silver top in Wisconsin (**35**). *Tarsonemus spirifex* Marchal was associated with a silver top of oats in Europe (**23**), but the gnarled, twisted base of the terminal internode distinguishes this trouble from American silver top. Various mites have been associated with white ear of grasses in Europe (**16**, **27**, **34**).

Stewart (**38**) discovered that shriveled grass stems were sometimes covered by mycelium of *Sporotrichum poae* Pk. By later combinations

the fungus is also known as *Fusarium poae* (Pk.) Wr. (**41**) and *F. tricinctum* (Cda.) emend. Snyd. and Hans. f. *poae* (Pk.) Snyd. and Hans. (**36**). However, use of the name *F. poae* for the fungus in this paper follows the recommendation of Sprague (**37**).

That *Siteroptes graminum* can complete its life cycle on *F. poae* and disseminate spores of the fungus has been demonstrated (**3, 6, 9, 12, 18, 35, 38, 40**).

Incrimination of *F. poae* as a causal agent of silver top prior to 1946 was based on circumstantial evidence, owing to the association of the fungus with dead grass stems and the fact that *F. poae* and *S. graminum* taken from grass stems caused carnation bud rot (**6, 12, 38**).

Fusarium poae was consistently isolated from grass stems killed by silver top (**18, 35**). Because silver top was produced by inoculating *Fusarium poae* into grass stems injured by needle punctures and the fungus was reisolated from killed stems, Keil (**18**) and Scholl (**35**) concluded that *F. poae* was the pathogen and mites were the disseminating agents (the modern theory). Keil (**18**) also produced silver top by releasing mites, *Siteroptes graminum,* from *F. poae* cultures on *Agrostis tenuis* Sibth. plants held in a moist chamber.

Control of silver top in *Festuca rubra* was obtained in Pennsylvania by spring burning (**17, 18, 28**) and by fall burning (**30**). DDT controlled silver top on *Festuca rubra* in Pennsylvania (**30**), on *Poa pratensis* in Iowa (**22**), and on *Festuca rubra* var. *commutata* in Oregon (**7, 8**). More recently other insecticides also have controlled the disease (**8**).

MATERIALS AND METHODS

Culms bearing silver-top-affected inflorescences were examined in infested fields. If the culms were free from other obvious diseases the roots were removed along with any soil and extraneous basal leaf material, and the otherwise complete culms were immediately placed in plastic bags. Tall culms were enclosed in a roll of paper. The majority of the collections were held at 2–5° C for 24 to 48 hours, while a few collections made during cool weather were left outdoors overnight. The grass culms remained fresh until they were dissected, usually the following day. The culms were examined closely in the laboratory and selected for typical silver-top symptoms.

Selected culms were cut just below and 5 to 6 inches above the affected node, leaving a culm segment consisting of the node and a portion of the leaf sheath enclosing the affected stem internode. The exterior of the leaf sheath was disinfected by wiping the surface with a

cotton pad slightly moistened with 95% ethanol. Excess disinfectant was avoided to prevent treatment of the stem tissues inside the sheath. A portion of the leaf sheath was removed with a sterile razor blade to expose the shriveled internode, which was then severed slightly above and below the injury. The resulting dissected internode segments, usually $\frac{1}{4}$ to $\frac{1}{2}$ inch in length, were half immersed in sterile Difco potato-dextrose agar (PDA) in Petri dishes.

Results were recorded after 24, 48, and 72 hours and as many additional times as seemed necessary to detect microorganisms that otherwise might be overgrown. The incubation period on PDA was never less than 14 days, and all plates with *Fusarium* colonies were saved for 1 month to permit enlargement and detection of any female mites (*Siteroptes graminum*) transferred with the stem segments. The same procedure was followed during 1958 except that no disinfectant was used.

RESULTS

PRELIMINARY STUDIES, 1953–1956. An estimated 40% of the inflorescences of hard fescue, *Festuca ovina* var. *duriuscula*, exhibited silver top in a field in Union county (eastern Oregon) during 1953. All affected stems collected during July of that year were infested with *Fusarium poae*. No mites were found, but their absence seemed explicable by the dryness of the stems. However, the mite *Siteroptes graminum* was not found during periods favorable for its collection despite careful examinations of hard fescue plants from the same field from 1954 to 1957 (**7**, **8**).

An outbreak of silver top in *Poa pratensis* occurred in Union county during 1955. Most of the shriveled stems were not rotted, remained bright straw color, and apparently contained few or no microorganisms.

Studies during 1956 were largely devoted to testing the effectiveness of insecticides, fall burning of fields, and other measures for controlling silver top and preventing continued severe losses in grass-seed crops. However, results of other work during 1956 were conspicuously at variance with the accepted explanation for the etiology of silver top; i.e., *Siteroptes graminum* was found too late in the season to have caused the primary damage to Chewings fescue stems and *Fusarium poae* was not consistently isolated from dead stems.

The absence of *Siteroptes graminum* in silver-top-affected culms of *Festuca ovina* var. *duriuscula* and *Poa pratensis* in eastern Oregon, absence of *Fusarium poae* in affected *P. pratensis* stems in eastern Oregon, and irregular association of *F. poae* with culms of *Festuca*

rubra var. *commutata* in western Oregon were interpreted as being important discrepancies between these observations and the commonly held theory that *F. poae* and *S. graminum* are the primary agents of silver top. Therefore, studies in 1957 and 1958 were expanded to determine the association of microorganisms with silver top.

TABLE 1

PREVALENCE OF MICROORGANISMS RECOVERED ON PDA FROM DAMAGED STEM TISSUES FROM SILVER-TOP-AFFECTED CULMS OF FESTUCA RUBRA VAR. COMMUTATA COLLECTED IN THREE FIELDS IN CLACKAMAS COUNTY, OREGON, 1957

Condition of dead panicles	Date stems planted on PDA	Number stems plated	Per cent of stems yielding				
			No organisms	*Fusarium poae*	Other fungi	Bacteria	*Siteroptes graminum*
Fields A and B:[a]							
Green	June 10	73	64.4	15.1	5.5	15.1	0.0
Green	June 19	6	50.0	0.0	50.0	0.0	0.0
Green	June 24	6	0.0	16.7	16.7	66.7	0.0
Total green, dead		85	58.8	14.1	9.4	17.6	0.0
White	June 1	96	61.5	13.5	14.6	14.6	0.0
White	June 6	41	34.1	36.6	19.5	19.5	2.4
White	June 10	247	49.8	30.8	8.9	11.7	12.1
White	June 19	150	13.3	16.7	34.0	33.3	2.6
Weathered white	June 19	20	10.0	25.0	35.0	30.0	0.0
White	June 24	105	37.1	21.0	21.0	24.8	1.0
Total white (fields A and B)		659	39.0	23.7	18.8	20.2	5.4
Field C:[b]							
White	June 1	7	100.0	0.0	0.0	0.0	0.0
White	June 4	20	80.0	0.0	0.0	20.0	0.0
White	June 12	55	80.0	3.6	1.8	14.5	0.0
White	June 19	20	40.0	5.0	15.0	35.0	0.0
Total field C		102	74.5	2.9	3.9	18.6	0.0

[a] Leaf growth thick and culms abundant.
[b] Leaves short and heading sparse.

STUDIES WITH *Festuca rubra* VAR. *commutata*, 1957. The major effort was directed to plants of *Festuca rubra* var. *commutata* in Clackamas county in western Oregon, because of the seriousness of silver top in this species. No microorganisms were recovered from tissues dissected from the terminal internode of 40 culms containing healthy, green panicles still in the boot or from 15 culms with emerged, healthy panicles.

Results obtained by plating damaged internode tissues from silver-top-affected culms of Chewings fescue plants collected at different dates in two commercial seed-production fields (fields A and B) are combined in TABLE 1. Plants in fields A and B were characterized by

abundant leaf growth and mid-season lodging of numerous culms. The incidence of *Fusarium poae* must be considered as relatively low for a pathogen, because this fungus usually is easily isolated. The low percentage recovery of *Siteroptes graminum* from stems with white panicles and complete absence of this organism in stems with green, dead panicles is strong evidence that this mite is not responsible for the dead inflorescences.

TABLE 2

PREVALENCE OF MICROORGANISMS RECOVERED ON PDA FROM SHRIVELED STEM TISSUES FROM SILVER-TOP-AFFECTED CULMS OF FESTUCA ARUNDINACEA, CLACKAMAS COUNTY, OREGON, 1957 AND 1958

Condition of dead panicles	Date stems planted on PDA	Number stems plated	Per cent of stems yielding				
			No organisms	*Fusarium poae*	Other fungi	Bacteria	*Siteroptes graminum*
During 1957:							
Green	June 10	6	83.3	0.0	16.6	0.0	0.0
Green	June 20	35	31.4	0.0	17.1	45.7	0.0
Total green		41	39.0	0.0	17.0	39.0	0.0
White	June 4	20	60.0	25.0	0.0	15.0	0.0
White	June 10	75	72.0	0.0	10.7	20.0	0.0
White	June 20	100	60.0	0.0	14.0	21.0	0.0
Total white		195	64.6	2.6	11.3	20.0	0.0
All panicles		236	60.2	2.1	12.3	23.3	0.0
During 1958:							
Green	June 5	30	26.7	6.7	20.0	63.3	0.0
White	June 5	20	45.0	5.0	10.0	50.0	0.0

Significant evidence against *Fusarium poae* as a primary agent in the etiology of silver top was obtained in studies of stems of Chewings fescue collected in a single location, Field C (TABLE 1). The absence of *F. poae* in samples collected June 1 and 4 and its very low incidence in samples collected June 12 and 19 from Field C compared with results from Fields A and B probably can be explained by the differences in field conditions. Field C was pastured late in the spring and was meagerly fertilized, and therefore a short growth of leaves similar to that of a clipped lawn and only a thin crop of panicles were present. Furthermore, culms remained erect and dried quickly after rains. Conditions in Field C were much less favorable for development of microorganisms around the culms than in Fields A and B.

Absence of *Siteroptes graminum* from all stems from Field C is regarded as significant evidence that the mite is not directly involved in

producing silver top. The results with Chewings fescue stems during 1957 demonstrate that silver top occurs in Oregon in this grass with only slight association of *F. poae* and *S. graminum.*

STUDIES WITH *Festuca arundinacea*, 1957. An old field of tall fescue (*Festuca arundinacea*) of the argonomic variety Alta, which had about 30 per cent silver top during 1955 and 1956, provided another opportunity for study of propitious material. A thin crop of seed culms and restricted leaf growth permitted good aeration, and culms dried quickly after rains. Also, the tall culms of this grass species held the damaged

TABLE 3

PREVALENCE OF MICROORGANISMS RECOVERED ON PDA FROM DAMAGED STEM TISSUES FROM SILVER-TOP-AFFECTED CULMS OF POA PRATENSIS FROM WESTERN OREGON, 1957

Condition of dead panicles	Date stems planted on PDA	Number stems plated	Per cent of stems yielding				
			No organisms	*Fusarium poae*	Other fungi	Bacteria	*Siteroptes graminum*
White[a]	May 17	11	54.4	0.0	27.2	27.2	0.0
White[b]	June 4	24	45.8	20.8	0.0	33.3	0.0
White[b]	June 13	45	48.8	35.5	2.2	13.3	0.0
White[b]	June 20	35	31.4	40.0	11.4	17.1	0.0
White[b]	June 20	12	25.0	41.6	25.0	8.3	0.0
White[c]	July 2	40	12.5	7.5	45.0	35.0	0.0
Total white		167	28.7	25.7	17.4	22.7	0.0
Green[b]	June 13	10	70.0	10.0	20.0	0.0	0.0
Total, all stems		177	31.0	24.8	17.5	21.5	0.0

[a] Row planting in Benton county, Field E.
[b] Shady location, Clackamas county, Field F.
[c] Open field in Clackamas county, Field G.

stem tissues well above the basal leaves. Thus, conditions in this field were much less favorable for development of microorganisms near the zone of stem injury than in most other fields studied. Therefore, the material from this field offered one of the best opportunities for detection of damaged stem tissues free from microorganisms. The results in TABLE 2 that show absence of *Fusarium poae* in stems with green dead panicles and extremely low incidence of the fungus in stems with white panicles demonstrate again that silver top can occur without this fungus. Complete freedom from *Siteroptes graminum* in all silver-top-affected culms of tall fescue is additional evidence that this mite is not involved.

STUDIES WITH *Poa pratensis*, 1957. Only limited material of *Poa pratensis* was collected during 1957; most stems studied had white

panicles. The results (TABLE 3) show an increase in incidence of *Fusarium poae* in Field F as the season advanced from 20.8 per cent of stems with white panicles collected June 4 to a high of 41.6 per cent of stems with white panicles collected June 20. The results in TABLE 3 are helpful in elucidating the relation of microorganisms to silver top, because material was collected from three different fields in which plant growth was widely different. *F. poae* was not recovered from stem tissues in culms collected May 17 in a row planting (Field E). The affected culms from common Kentucky-bluegrass-type plants were taller

TABLE 4

PREVALENCE OF MICROORGANISMS RECOVERED ON PDA FROM DAMAGED STEM TISSUE FROM SILVER-TOP-AFFECTED CULMS OF FESTUCA RUBRA VAR. COMMUTATA FROM 4 FIELDS IN CLACKAMAS COUNTY, OREGON, 1958

Condition of dead panicles	Date stems planted on PDA	Number stems plated	Per cent of stems yielding				
			No organisms	*Fusarium poae*	Other fungi	Bacteria	*Siteroptes graminum*
Green	May 23	55	45.5	10.9	12.7	40.0	7.3
Green	June 5	128	35.2	10.9	20.3	44.5	0.8
Total green		183	38.3	10.9	18.0	43.2	2.7
White	May 23	15	33.3	40.0	13.3	20.0	33.3
White	June 5	35	45.7	37.1	5.7	8.6	5.7
White, discolored	June 11	105	1.9	18.1	35.2	78.1	1.0
Dirty white, culm dry	July 7	25	0.0	60.0	40.0	100.0	8.0
Total white		180	12.8	29.4	28.3	62.8	5.6
Total, all stems		363	25.6	20.1	23.1	52.9	4.1

than the main crop of Merion Kentucky bluegrass. The fungus was obtained from only 7.5 per cent of the injured stems collected in another location with good aeration owing to a thin stand (Field G). The low incidences of *F. poae* in these two locations (Fields E and G) contrast sharply with the much higher incidence of the fungus in culms collected in a shady, moist location (Field F) in which conditions were more favorable for microorganisms.

Absence of *Siteroptes graminum* from all the 177 stems of *Poa pratensis* studied in 1957 was surprising, especially from plant material from the shady location (Field F) in which the sod was old and had a dense growth of leaves. Absence of the mite is also interesting, because *P. pratensis* was the main grass species with which both *F. poae* and *S. graminum* were associated in earlier silver-top studies conducted in eastern United States.

STUDIES WITH *Festuca rubra* VAR. *commutata*, 1958. Results of plating damaged internode tissues from silver-top-affected culms of Chewings fescue are summarized in TABLE 4. Recovery of *Fusarium poae* from only 10.9 per cent of the stems with dead, green panicles collected May 23 and June 5 contrasts sharply with the much higher percentage recovery of the fungus from stems with white panicles collected on the same, and later, dates. The results are comparable with those for 1957, showing a gradual increase in incidence of *F. poae* in dead stem tissues the longer they are exposed to invasion by microorganisms.

TABLE 5

PREVALENCE OF MICROORGANISMS RECOVERED ON PDA FROM TISSUES OF POA PRATENSIS CULMS AFFECTED WITH SILVER TOP, COLLECTED IN FOUR FIELDS IN CLACKAMAS COUNTY IN WESTERN OREGON AND ONE LOCATION IN UNION COUNTY IN EASTERN OREGON, 1958

Condition of dead panicles	Date stems planted on PDA	Number stems plated	Per cent of stems yielding				
			No organisms	*Fusarium poae*	Other fungi	Bacteria	*Siteroptes graminum*
From western Oregon:							
Green	May 16	105	58.1	2.9	13.3	28.6	2.9
Green and partly green	May 23	190	58.4	2.6	8.4	31.6	0.5
Green and partly green	June 5	38	10.5	7.9	26.3	65.8	7.9
Total green		333	52.9	3.3	12.0	34.5	2.1
White	May 23	150	40.7	2.0	13.3	48.0	0.0
White, discolored	June 5	135	14.8	4.4	29.6	73.3	0.0
White, discolored	June 11	80	2.5	26.3	41.3	81.3	0.0
White, dirty	July 7	20	0.0	25.0	55.0	95.0	12.0
Total white		385	21.6	7.8	27.0	66.2	0.8
Total all panicles		718	36.1	5.7	20.1	51.5	1.4
From eastern Oregon:							
Bright white	May 20	50	92.0	0.0	2.0	6.0	0.0

A more rapid increase in the incidence of bacteria and other fungi was also noted in stems collected during 1958 from Chewings fescue than in those collected previously. Yet *S. graminum* was recovered from only 4.1 per cent of all stems studied. As in 1957 a great variety of bacteria and other fungi were recovered from Chewings fescue stems.

The four fields of Chewings fescue studied in 1958 were characterized by thick stands, heavy leaf growth and numerous panicles, resulting in moist conditions favorable for development of microorganisms. Therefore, the incidence of microorganisms associated with dead stems of Chewings fescue with green panicles during 1958 must be considered as

remarkably low. Recovery of *Fusarium poae* from 40 per cent of stems with white panicles collected May 23 (TABLE 4) compared with only 10.9 per cent of stems with green, dead panicles collected on the same date suggests that if the fungus quickly invades dead stems in humid areas, detection of the silver-top-damaged stems free of microorganisms may be difficult. Thus, isolation from stems with old, white panicles probably would result in recovery of *F. poae* from a high percentage of stems and could lead to the conclusion that the fungus was the causal agent.

STUDIES WITH *Poa pratensis,* 1958. Prevalence of microorganisms in silver-top-affected stems of *Poa pratensis* collected during 1958 in four fields is summarized in TABLE 5. The extremely low incidence of *Fusarium poae* in stems with green, dead panicles collected on three dates and even in stems with white panicles collected May 23 and June 5 is remarkable, because the growth of Kentucky bluegrass was dense and favored development of microorganisms at each location.

The freedom from microorganisms in 58 per cent of the stems collected May 16 and May 23 is also regarded as strong evidence against all microorganisms recoverable on PDA as causal agents. The other fungi and bacteria recovered from *P. pratensis* stems again were of a great variety.

Appearance of *Siteroptes graminum* in the bluegrass stems was mainly confined to samples from two of the four fields studied. The low incidence in all stems (1.4 per cent) and absence in one of the locations must be considered as evidence against the mite as a primary agent.

Fifty culms of *Poa pratensis* affected with typical silver top were collected in eastern Oregon, May 19, and segments of damaged internodes were plated on PDA, May 20. The stem segments remained free from *Fusarium poae* and *Siteroptes graminum* (TABLE 5), and 92 per cent of the stems remained sterile on PDA for 1 month. These results are similar to those obtained in studies with bluegrass culms during 1955 from eastern Oregon and demonstrate that silver top in low-rainfall areas occurs independently of microorganisms.

STUDIES WITH *Festuca arundinacea,* 1958. Results from plating limited numbers of affected culms of *Festuca arundinacea* collected in 1958 are shown in TABLE 2. The incidence of microorganisms was slightly higher in 1958 than in 1957 and probably is explained by more favorable conditions for their development in the different location. The absence of *Siteroptes graminum* is particularly notable because the tall fescue specimens were collected in the same location where most of the mite-infested culms of *Poa pratensis* were collected (TABLE 5).

DISCUSSION

The long-held theory that silver top is a disease caused by *Fusarium poae* is challenged by the general lack of association of the fungus in the present study. Detection of damaged grass stems free from *F. poae* was due partly to collection of samples soon after death of inflorescences and before invasion by secondary organisms. However, the rate of invasion of dead stems by microorganisms may be slower in western Oregon owing to much drier climatic conditions during the spring than in middlewestern and eastern states where most previous studies were made. Eastern Oregon is characterized by even less rainfall and lower humidities during the spring. The gradual increase in incidence of microorganisms in dead grass stems the longer they are exposed to invasion offers a possible explanation for the more frequent association of *F. poae* in previous studies made in humid areas.

The ease with which *F. poae* is recovered from plant tissues should be considered in evaluating any silver-top study. Sprague (**37**), after inoculation trials on grasses, concluded that isolates of *F. poae* are comparatively weak parasites or saprophytes. In the present silver-top studies, *F. poae* was quickly isolated in the presence of assorted molds and bacteria, and even when all the stems contained bacteria (TABLE 4). *F. poae* is apparently a strong competitor among saprophytic organisms, as shown by its prevalence in old dead stems, and if present in grass stems affected with silver top, the fungus should seldom be difficult to recover.

Because the results in the present paper are diametrically opposed to the theory that *Fusarium poae* and *Siteroptes graminum* are the causal agents of silver top, the literature was carefully searched, but no evidence was found to justify this theory prior to 1946. To the contrary, establishment of *F. poae* as the causal agent of silver top appears to have arisen under questionable circumstances. In the first paper to suggest that *F. poae* might cause silver top, Stewart and Hodgkiss (**38**) did not prove a causative role for the fungus. Instead, they stated (p. 93): "For a time it was suspected that the *Sporotrichum* [*F. poae*] might be one of the causes of silver top, but this idea was subsequently abandoned when it was found that in the majority of cases the affected culms were quite free from *Sporotrichum* or other fungus. However, both the *Sporotrichum* and the mite reappeared to a limited extent about Geneva in 1903, 1905, 1907, and 1908; also at Interlaken, New York, in 1907. In one instance, the *Sporotrichum* and associated mite were found on timothy, *Phleum pratense* L., affected with silver top." Ap-

parently, Stewart and Hodgkiss were doubtful whether *F. poae* was the causal agent; but in the same bulletin, after discussing the carnation bud rot and their hypothesis that *Siteroptes graminum* carries the fungus into carnation buds on its way to feed, with resulting fungus infection of the buds, they stated (p. 115): "The above applies especially to carnations. Probably it applies also to June grass, but the association of the mite and fungus on June grass seems to be much less constant."

Although Stewart and Hodgkiss provided no good evidence that *F. poae* was the chief causal agent of silver top, their work has been cited as supporting the relationship. Absence of *F. poae* from silver-top-affected stems in New York (**38**) apparently was confirmed some 20 years later by Horsfall (**13**, p. 115), who reported, "Several attempts to culture the fungus failed." Thus, after the suggestion, on the basis of circumstantial evidence, by Stewart and Hodgkiss (**38**) that *F. poae* might be the causal agent, subsequent workers apparently have not considered the possibility that this fungus could be a secondary invader of dead internodes.

The few other reports on absence of microorganisms from affected stems also are seldom mentioned in later literature. Osborn (**24**) reported in 1891 that fungi were rarely seen in tissues of stems of grasses in Iowa, and Reuter (**33**) concluded in 1900 that during rainy periods mold fungi were secondary invaders of mite wounds in Finland. Kirchner (**19**) announced that a *Sporotrichum* was associated with affected culms of oats, but that *Tarsonemus spirifex* [= *Steneotarsonemus spirifex* (Marchal)] was the primary agent responsible. Stewart and Hodgkiss (**38**) also noted that *Fusarium poae* and *Siteroptes graminum* were more constantly associated with short culms of *Poa pratensis* where moisture was more favorable than with taller culms.

Keil (**18**) and Scholl (**35**) reported that *Fusarium poae*, when inoculated into needle punctures in grass culms, invaded the stem tissues and killed the stem and inflorescence, thereby causing a silver top. Because Keil and Scholl reisolated *F. poae* from inoculated stems, they concluded that this evidence of pathogenicity demonstrated that the fungus was the causal agent of silver top.

Keil (**18**) produced silver top by releasing numbers of *Siteroptes graminum* from cultures of *F. poae* on plants of *Agrostis tenuis* Sibth. held in a moist chamber, whereas uninoculated plants had no dead panicles. However, the killing of panicles by the combination of the mite and fungus could have resulted from fungus invasion of stems already wounded by insects, because the plants used in the experiment were not removed from the field until the flowering stage. *F. poae* and *S.*

graminum also apparently killed smut-infected culms of barley among crowded plants in a greenhouse and under moist conditions in the field, as reported by Cherewick and Robinson (**3**). However, their results are not applicable to silver top, because the mite and fungus did not damage smut-free barley culms. Although these two reports cannot be accepted as proof that *F. poae* and *S. graminum* are primary agents causing silver top, the work suggests the possibility that, in humid areas with sufficient rainfall, especially during April, May and June, *F. poae* may invade insect wounds in grass stems and contribute to the killing of otherwise mildly wounded stems.

Many workers have reported association of *Siteroptes graminum* with dead grass culms, and a few have indicated that the mite was primarily responsible. However, the relation to silver top of *S. graminum* has been puzzling ever since control of the disorder by DDT was first reported (**30**), because this chemical is usually a poor mitacide (**2**). The absence of *S. graminum* in most of the grass stems in the present study is subject to several criticisms, e.g., much of the plant material was held near freezing (2–5°), though moist, for 24 to 48 hours before internode segments were plated on PDA; only a fraction of the total stem was plated; and detaching culms from the roots may have disturbed the mites, resulting in migration from the zone of injury. These objections are partly removed by the absence of immobile, swollen females in the material studied, since only two were apparent in the numerous stems studied during 1957 and 1958.

Interpretation of the results in Oregon as evidence of the unimportance of the mite is supported by the fact that *S. graminum* was not controlled by as much as 10 pounds of actual DDT per acre in laboratory tests (**20**). Therefore, nearly complete elimination of silver top by ½ to 1 pound actual DDT in grass fields should exonerate *S. graminum* as a primary agent of silver top in Iowa, Pennsylvania, and Oregon. Control of silver top by DDT possibly also exonerates many other mites associated with affected grass stems. However, the culm damage caused by *Stenotarsonemus* (*Tarsonemus*) *spirifex* and perhaps certain other species should be distinguished from silver top by the greatly different symptoms.

Although microorganisms occasionally may contribute to death of grass stems in humid areas, their absence in most silver-top-affected culms of grasses in Oregon challenges the commonly held theory that *Fusarium poae* and *Siteroptes graminum* are the primary causal agents of a disease. Instead, the results described here, a revaluation of the

literature, and control by DDT are interpreted as evidence dictating a return to insects as the primary agents causing silver top of grasses.

Among the insects reported in association with affected grass culms, several species of thrips appear to be among the most likely causes of silver top. *Anaphothrips obscurus* (Müll.) was accepted as the causal agent of silver top in New England after the comprehensive work by Hinds (**11**) and in southern Canada by Hewitt (**10**). *Aptinothrips rufus* (Gmelin) and *A. stylifer* Trybom are associated with the disorder in Oregon (**7**, **8**), but the exact relation of these thrips to the etiology of silver top remains to be determined.

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LITERATURE CITED

1. **Alfaro, A.** 1946. El acaro *Pediculopsis graminum* Reut. y el hongo *Nigrospora oryzae* (Berk. et Br.) Petch, en asociacion parasitaria sobre Tigos aragonese. Bol. Pat. Veg. Ent. Agric Madr. **16**: 321–334. *12* figs. 1946. (Abstract in Rev. Appl. Myc. **26**: 388. 1947.)
2. **Baker, E. W., and G. W. Wharton.** 1952. An Introduction to Acarology. Macmillan, New York. 465 pp.
3. **Cherewick, W. J., and A. G. Robinson.** 1958. A rot of smutted inflorescences of cereals by *Fusarium poae* in association with the mite *Siteroptes graminum*. Phytopathology **48**: 232–234.
4. **Comstock, J. H.** 1875. Notes on entomology: A syllabus of a course of lectures delivered at the Cornell University. 154 pp. University Press, Ithaca, N. Y.
5. **Comstock, J. H.** 1888. The grass-eating thrips. Amer. Nat. **22**: 260–261.
6. **Cooper, K. W.** 1940. Relations of *Pediculopsis graminum* and *Fusarium poae* to central bud rot of carnations. Phytopathology **30**: 853–859.
7. **Hardison, J. R., and G. W. Krantz.** 1957. Progress report on silver top of grasses in 1956. Oregon Seed Growers League, Proc. 16th Annual Meeting (Dec. 1956): 57, 59, 60.
8. ——, **G. W. Krantz, and E. A. Dickason.** 1958. Progress report on silver top of grasses for 1957. Oregon Seed Growers League, Proc. 17th Annual Meeting (Dec. 1957): 87, 89–91.
9. **Heald, F. D.** 1908. The bud-rot of carnations. Nebr. Agr. Exp. Sta. Bul. 103.
10. **Hewitt, C. Gordon.** 1914. Sterility in oats caused by thrips. Jour. Econ. Entomol. **7**: 211–218.
11. **Hinds, W. E.** 1900. The grass thrips. Mass. Ag. Coll. 25 pp.
12. **Hodgkiss, H. E.** 1908. Notes on the grass mite, *Pediculopsis graminum* Reuter. Jour. Econ. Entomol. **1**: 375–377.
13. **Horsfall, J. G.** 1930. A study of meadow crop diseases in New York. N. Y. (Cornell) Agr. Exp. Sta. Mem. 130.

14. **Hukkinen, Y.** 1934. Ueber die Weissährigkeit der Gramineen. I. Streit über die Thysanopteren als Weissährigkeitserreger. Maataloust. Aikakausk. **6**: 139–158. *2 figs.* Helsingfors. (With a Summary in Finnish.) (Abstract in Rev. Appl. Ent. A. **23**: 261. 1935.)
15. **Jewett, H. H., and J. T. Spencer.** 1944. The plant bugs, *Mirus dolobratus* L., and *Amblytylus nasutus* Kirschbaum, and their injury to Kentucky bluegrass, *Poa pratensis* Linn. Jour. Amer. Soc. Agron. **36**: 147–151.
16. **Kaufmann, O.** 1925. Die Weissährigkeit der Wiesengräser und ihre Bekämpfung. Arb. Biol. Reichsanst. Land- Forstw. Berlin **13**: 497–567. (Abstract in Rev. Appl. Ent. 3. **13**: 396. 1925.)
17. **Keil, H. L.** 1940. Control of silver top by burning. U. S. D. A. Pl. Dis. Rep. **26**: 11.
18. ——. 1946. White-heads of Grasses. Doctorate thesis, Pennsylvania State College. 37 pp.
19. **Kirchner, Von O.** 1904. Eine Milbenkrankheit des Hafers. Zeits. Pflanzenkrank. **14**: 13–18.
20. **Krantz, G. W.** 1956. Relationship of the mite *Pediculopsis graminum* Reut. to silver top disease of Oregon grasses. Oregon Agr. Exp. Sta. Report of Project No. 291, p. 5. Unpublished.
21. **Leach, J. G.** 1940. Insect Transmission of Plant Diseases. McGraw-Hill, New York. 615 pp.
22. **Lilly, J. H.** 1956. Pest control in hay and pasture crops. Iowa Farm Science **10**: 3–4.
23. **Marchal, Paul.** 1902. Les Tarsonemus des Graminées. Description d'une espece nouvelle vivant sur l'Avoine. Bul. Soc. Ent. France **4**: 98–104.
24. **Osborn, H.** 1891. Silver-top in grass and the insects which may produce it. Canad. Ent. **23**: 93–96.
25. ——. 1918. The meadow plant bug, *Mirus dolobratus*. Jour. Agr. Res. **15**: 175–201.
26. ——. 1939. Meadow and Pasture Insects. Educator's Press, Columbus, Ohio. 288 pp.
27. **[Ovchinnikova, (M. I.).]** [*Pediculopsis graminum* E. Reut. as a pest of cereal grasses.] (In Russian.) Plant Prot. no. 16: 99–107. Leningrad. 1938. (Abstract in Rev. Appl. Ent. A. **27**: 151–152. 1939.)
28. **Pennsylvania Agricultural Experiment Station.** Fifty-sixth Annual Report. Bulletin 446. 1943.
29. ——. Sixtieth Annual Report. Bulletin 488. 1947.
30. ——. Sixty-first Annual Report. Bulletin 502. 1948.
31. **Pohjakallio, O.** 1936. Valkotähkäisyystutkimuksia Jokioisissa kesällä 1935. [Investigations on white ear conducted at Jokioinen in the summer of 1935.] Valt. Maatalousk. Julk. 77, 78 pp. (Finnish, with German summary.) (Abstract in Rev. Appl. Myc. **16**: 31. 1937.)
32. **Rademacher, B.** 1936. Flissigkeit, Blasenfuss-Schaden und Fritlfliegenbefall an Haferrispen. Kranke Pflanze **13**(7–8): 129–132. Dresden. (Abstract in Rev. Appl. Ent. A. **24**: 623. 1936.)
33. **Reuter, E.** 1900. Über die Weissährigkeit der Wiessengrässer in Finland. Ein Beitrag zur Kenntnis ihrer Ursachen. Act. Soct. Fauna Flora Fenn. **19**: 1–136. (Abstract in Ztschr. Pflanzenkrank. **11**: 250–253. 1901.)

34. **[Sakharov, (N. L.).]** 1939. [On the causes of white-ear in cereals.] (In Russian.) Plant Prot. no. 18: 52-60. Leningrad. (With a summary in English.) (Abstract in Rev. Appl. Ent. A. **27**: 680. 1939.)

35. **Scholl, J. M.** 1947. Studies of certain factors affecting seed production and the yield and composition of the forage of some common grasses. Doctorate thesis, University of Wisconsin. 47 pp.

36. **Snyder, W. C., and H. N. Hansen.** 1945. The species concept in Fusarium with reference to Discolor and other sections. Amer. Jour. Bot. **32**: 658-666.

37. **Sprague, R.** 1950. Diseases of Cereals and Grasses in North America. Ronald Press, New York. 538 pp.

38. **Stewart, F. C., and H. E. Hodgkiss.** 1908. The Sporotrichum bud-rot of carnations and the silver top of June grass. N. Y. Agr. Exp. Sta. Techn. Bul. 7: 83-119.

39. **Webster, F. M.** 1889. Notes on some species of insects which affect the upper portion of the stems of some grasses. Insect Life **1**: 372-374.

40. **Wolcott, Robert H.** 1908. A mite accompanying the bud-rot of carnations. Nebr. Agr. Exp. Sta. Bul. 103.

41. **Wollenweber, H. W., and O. A. Reinking.** 1935. Die Fusarien, ihre Beschreibung, Schadwirkung und Bekämpfung. Parey. Berlin. 355 pp.

42. **Zacher, F.** 1919. Die Weissährigkeit der Wiesengrässer. Deutsche Landwirtschftl. Presse, Berlin **46**: 445-446. *7 figs.* (Abstract in Rev. Appl. Ent. **7**: 455. 1919.)

A NEW SPECIES OF MASTIGOSPORIUM FROM TROPICAL SOIL

R. H. Petersen

(with 18 figures)

While isolating fungi from soil samples obtained in the South Pacific area by Dr. L. S. Olive in 1956, the writer discovered an interesting phragmosporous fungus with white mycelium. Upon attempting the identification of this organism, it was soon found that, while quite definitely related to the genus *Mastigosporium*, the organism was considerably different from all known species (Hughes, **1951**).

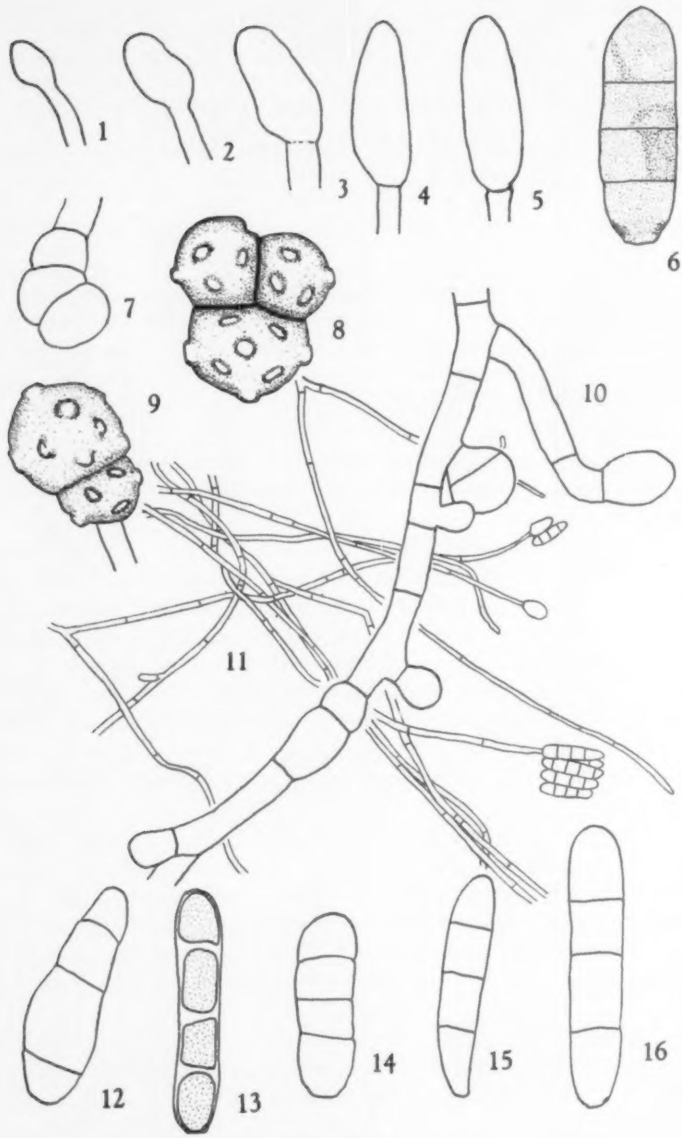
Only one species of *Mastigosporium* was found to appear similar to the new organism, that being *Mastigosporium rubricosum* (Dearn. and Barth.) Sprague.

Sprague (**1938**) briefly described the colonies of *M. rubricosum* (= *M. calvum*) on various media. Only on Mix's agar was the colony white. In all cases the colonies were flattened, leathery, and wrinkled. The new organism, on several agars tested (Czapek's, potato-dextrose, and rose-bengal–streptomycin agars), formed floccose, rapidly spreading, white colonies with an abundance of spores. Only on corn meal agar (with 0.1% yeast extract) was the mycelium partially submerged, but even in this instance, the conidiophores were scattered over the whole mycelium, and not clumped as described as being characteristic of the genus.

Growth on potato-dextrose agar was rapid, single-conidial inoculation reaching a diameter of one centimeter in 48 hours and 3–4 centimeters in one week, as contrasted to the much slower growth of previously described species. In the description of the latter, no mention was made of any production of chlamydospores. The new organism, after some time in culture, produces 1–3-celled chlamydospores of rather striking appearance.

While the conidia of both *M. rubricosum* and the new organism are usually three-septate, the size of the spores differs considerably. Bollard (**1950**) lists spore measurements as follows:

M. rubricosum from *Dactylis glomerata*—from leaves: 31–59 μ; from culture: 33–51 μ.



FIGS. 1–16.

M. rubricosum from *Agrostis stolonifera*—from leaves: 35–45 μ; from cultures: 35–53 μ.

The conidia of the new species are considerably smaller, being 20–25 μ long. It is possible that if the new species is phytopathological, the conidia from the host might be larger. However, even an increase proportional to that in *M. rubricosum* would not approximate the spore size of that species.

The following new species is therefore proposed:

Mastigosporium heterosporum sp. nov.

Caespitulis albis vel laete coloratis; hyphis ramosis, septatis, hyalinis; hyphis fertilibus erectis vel ascendentibus, attenuatis ad conidiorum basim, parce septatis, 80–140 × 3.5–4.9 μ; conidiis in ordine productis, a latere fasciculatim collectis, 1–4 (vulgo 3) -septatis, hyalinis, brevi-cylindraceis cum terminibus rotundis, haud constrictis vel septis aliquanto constrictis, 20–25 × 6.0–6.5 μ. Fungus maturior chlamydosporas tuberculatas, 2–3-cellulares, vulgo terminales vel in brevibus ramis, 11–14 × 7.5–8.5 μ producens.

Mycelium branching, septate, hyaline; conidiophores erect or ascending, tapering to the base of the conidia, sparsely septate, 80–140 × 3.5–4.9 μ long; conidia produced successively, collecting in lateral fascicles, 1–4 (usually 3) -septate, hyaline, short-cylindric with rounded ends, smooth or slightly constricted at the septa, 20–25 × 6.0–6.5 μ; older cultures producing 2–3-celled chlamydospores, tuberculate and yellow, usually terminal or on short lateral branches, 11–14 × 7.5–8.5 μ.

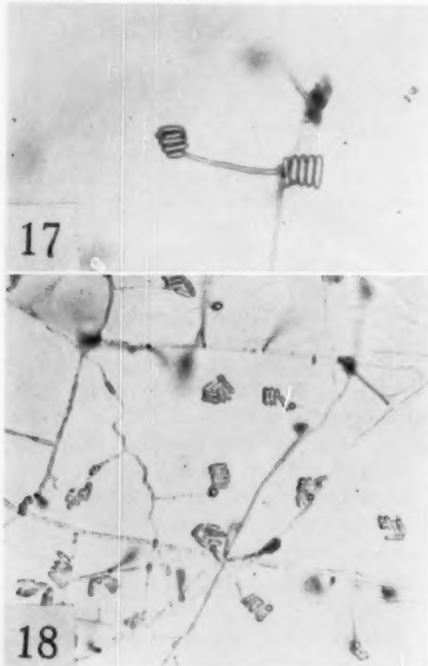
The type location is designated as moist soil, in a river bed, Paea District, Tahiti. The specific epithet refers to the production of chalmydospores as well as conidia.

Conidium production is essentially the same as that described for *Mastigosporium* by Bollard (**1950**). The conidiophore apex swells, and then is separated from the conidiophore by a septum (FIGS. 1–5). The conidium continues to swell, forming from one to four septa before reaching maturity (FIGS. 6, 12–16). When the conidium is mature, another conidial primordium appears, pushing the old conidium to one side. This process continues until a row of laterally aligned spores is produced with only the youngest spore still attached to the tip of the

Mastiogosporium heterosporum. FIGS. 1, 2. Conidial primordia. FIG. 3. Septum formation. FIG. 4. Conidium of mature size on conidiophore prior to septum formation. FIG. 5. Conidium on conidiophore, showing slight collar occasionally found. FIG. 6. Mature conidium. FIGS. 7–9. Chlamydospores. FIG. 10. Immature chlamydospores on hypha. FIG. 11. Portion of mycelium showing conidium production. FIGS. 12–16. Mature septate conidia. FIGS. 1–10, 12–16, × 700. FIG. 11, × 100.

conidiophore. Hence, a peculiar kind of head, not previously described for the genus, is developed. The series may be composed of as many as 10–12 conidia, presenting a rather striking appearance (FIGS. 11, 17, 18).

After weeks in culture, when the medium begins to dry, chlamydospores are produced (FIG. 10). They are 2–3-celled (most commonly



Mastigosporium heterosporum. FIG. 17. Conidium production, showing conidium aggregation. FIG. 18. Conidium and chlamydospore production. Both × 60.

two-celled) and are usually produced terminally or on short lateral branches, although occasionally intercalary chlamydospores have been observed. Quite prominent warts are formed after the chlamydospores have reached maturity. These warts are up to 0.5 μ in height, and are formed on the outside wall of the chlamydospore. The chlamydospores are golden yellow in color and are able to withstand several weeks of drying at room temperature (FIGS. 7–9). Upon aging, the conidia degenerate, and their cells are often empty.

In no instance were any structures observed which resembled sclerotia. The hyphae were never observed to clump into aggregates. Finally, whereas all previously known species were described on grasses, *M. heterosporum* was isolated from soil. However, this does not eliminate the possibility that the new species may occur as a phytopathogen in nature.

Cultures of *M. heterosporum* have been deposited in the American Type Culture Collection, Washington, D. C., and at the Culturbureau at Baarn, Holland. Dried material is on deposit in the Mycological Collections of the New York Botanical Garden, and of the United States Department of Agriculture at Beltsville, Maryland.

The writer wishes to express his thanks to Dr. L. S. Olive of Columbia University, for his advice during the course of this study; and to Dr. Roderick Sprague for his advice on the new organism and the taxonomy of the genus.

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LITERATURE CITED

Bollard, E. G. 1950. Studies on the genus *Mastigosporium*. I. General account of the species and their host ranges. II. Parasitism. Brit. Myc. Soc. Trans. **33**: 250–275.

Hughes, S. J. 1951. Studies on microfungi. III. *Mastigosporium, Camposporium*, and *Ceratophorum*. Commonwealth Mycol. Inst. Mycol. Pap. 36.

Sprague, R. 1938. Two *Mastigosporium* leaf spots on Gramineae. Jour. Agr. Res. **57**: 287–299.

THE GENUS BERKLEASMIUM

ROYALL T. MOORE [1]

(WITH 21 FIGURES)

In a previous paper (**4**) the genus *Berkleasmium* was reestablished for certain sporodochial Deuteromycetes that had been immixed in *Sporidesmium* sensu Saccardo. The completion of an extensive examination of available material of the species ascribed to *Sporidesmium* has evinced a total of ten species that are considered to belong properly in *Berkleasmium.* The following key to these species is intended to provide a comprehensive description of each species, and the ensuing section provides the formal taxonomy and additional notes. On the line immediately below each specific entry is a formula in brackets that sets forth the key steps that encompass the description of the species, so that for any given species the description may be read through with ease. The species have been listed alphabetically. Finally, since the conidia were often stained or bleached to show better certain characters, and since this intention was often furthered in the photographic reproduction, the caution is extended that the degree of darkness apparent in the figures is not a true index of the degree of pigmentation.

BERKLEASMIUM Zobel

Colonies sporodochia; conidia phaeodictyous, borne monacrogenously on short, simple conidiophores, or else sessile.

TYPE: *Sporidesmium concinnum* Berkeley.

KEY TO THE SPECIES OF BERKLEASMIUM

1. Conidia deeply pigmented, fuscous to opaque, multicellular....................3
1. Conidia lightly pigmented, melleous....................2
  2. Conidia paucicellular, less than 15 cells....................8
  2. Conidia multicellular, many more than 15 cells....................9
3. Conidia, at least some, with subtending cells....................7
3. Conidia without subtending cells....................4
  4. Conidia fuscous to subopaque, but to some degree translucent....................6
  4. Conidia opaque....................5

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5. Conidia small, 8–14 × 10–18 μ, tuberculate to more or less scabrid, broadly oval to spherical or pyriform, at maturity sometimes slightly constricted at the septa; borne on short conidiophores, 4–6 μ long . . . . *triglochinis*
5. Conidia large, (26–)31–41.5(–52) × (41.5–)52–83(–99) μ, verrucose, subglobose to oval-ellipsoid, (elongate conidia sometimes strongly constricted), somewhat amorphous, sessile . . . . *opacum*
    6. Conidia cylindrical to slightly obclavate, sometimes somewhat curved, fuscous, sessile, 18.5–24 × 65–89.5 μ . . . . *lingula*
    6. Conidia oval to ovate, deep fuscous, borne on short stem-like conidiophores, 26–47 × 36.5–99 μ . . . . *conglobatum*
7. Subtending cells either numerous (volume sometimes exceeding primary portion), melleous, tending to be amorphous, or represented by a single, large, hyaline, globose to elliptical vesicle, or in some conidia absent; primary portion fuscous, constant in shape, moriform, (15.5–)18.5–22 × (18.5–)23.5–26.5(–31.5) μ . . . . *moriforme*
7. Subtending cells rarely more than one or two, absent on some conidia, hyaline; primary portion globose to subglobose to ovate or obovate, deep fuscous, 18.5–26 × (18.5–)26.5–34 μ . . . . *corticola*
    8. Conidia clavate to subclavate to subglobose, base truncate, moderately constricted at the septa, tending to be somewhat amorphous, borne on conidiophores of a few cells, laevigate, 13–18.5 × 26.5–39.5(–45) μ . . *vogelianum*
    8. Conidia subglobose to squarish-subglobose to oval-ellipsoid, not infrequently strongly constricted at a prominent medial septum with each moiety less prominently subdivided, sessile, surface minutely roughened, 8.5–11.5(–13) × 11.5–17 μ . . . . *minutissimum*
9. Profile regular, conidia elongate-dacryoid, cells large and fairly regular, 23.5–30 × 60–105 μ . . . . *concinnum*
9. Profile irregular, conidia subglobose to oval to irregular-cylindrical, composed of heteromorphic cells irregularly ordered, 16.5–18.5(–35) × 29–66 μ . . . . *granulosum*

BERKLEASMIUM CONCINNUM (Berk.) Moore (**4**). FIG. 6

[*1*, *2*, 9]

BERKLEASMIUM CONGLOBATUM (Cke. & Ell.) Moore (**4**). FIG. 5

[1, *3*, 4, *6*]

Berkleasmium corticola (Karst.) comb. nov. FIGS. 1–4

[1, 3, *7*]

≡ *Sporidesmium moriforme* Peck subsp. *corticolum* Karsten, Medell. Soc. Fauna Fl. Fenn. **14**: 99. 1887.

Material examined: H (Karsten coll.), TYPE, on old birch bark, Finland (slides RTM 1:258, E. G. Simmons X-11).

BERKLEASMIUM GRANULOSUM (Dur. & Mont.) Moore (**4**). FIG. 21

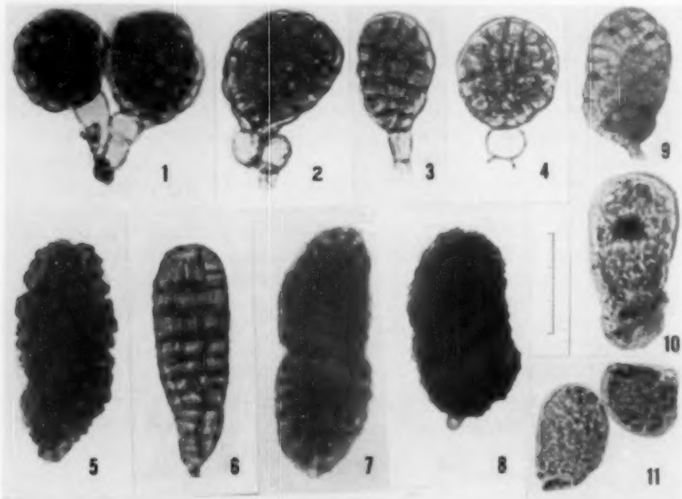
[*1*, *2*, *9*]

Berkleasmium lingula sp. nov. FIG. 20

[1, *3*, 4, 6]

Conidia multicellularia, cylindrica vel leviter obclavata, interdum nonnihil curvata, fusca, sessilia, 18.5–24.0 × 65.0–89.5 μ.

Ad lignum putridum, U.S.A., South Carolina, in Herb. FH (*Curtis no. 1787*, TYPUS; praeparatio microscopica RTM I:22, ISOTYPUS). Nomen specificum a cell. Berkeley et Curtis conditum, ab iis autem haud vulgatum et sub genero *Sporidesmio* sumptum.



FIGS. 1–4. *B. corticola,* conidial types (slide EGS X-11). FIG. 5. *B. conglobatum,* conidium. FIG. 6. *B. concinnum,* conidium. FIGS. 7, 8. *B. opacum,* conidia (slide RTM I:210). FIGS. 9–11. *S. rauii,* conidia (9, SCD slide; 10, 11, slide RTM I:247). Uniform magnification; scale in micra.

Berkleasmium minutissimum (Peck) comb. nov. FIGS. 17, 18

[*1*, 2, *8*]

≡ *Sporidesmium minutissimum* Peck, Bot. Gaz. **5**: 34. 1880.

Material examined: NYS, on dead wood, Vermont, leg. *C. G. Pringle* (383), TYPE (slide RTM I:225).

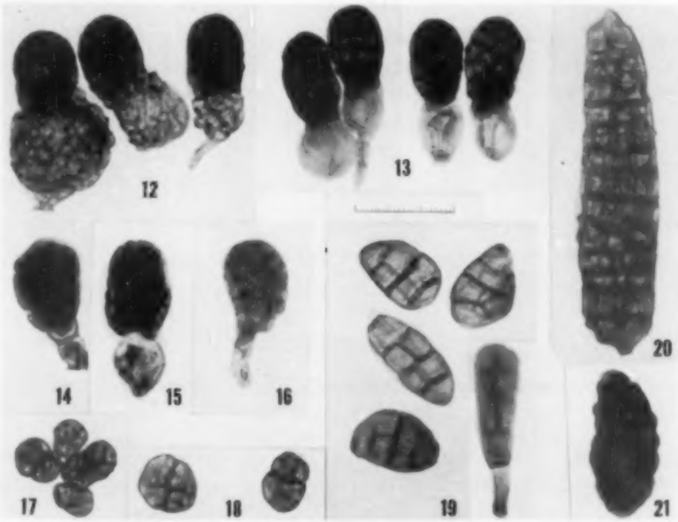
Berkleasmium moriforme (Peck) comb. nov. FIGS. 12–16

[1, 3, *7*]

≡ *Sporidesmium moriforme* Peck, N. Y. State Mus. Ann. Rept. **25**: 89. 1872.

= *Sporidesmium moriforme* Peck var. *ampelinum* Saccardo. Ann. Myc. **3**: 170. 1905.

These taxa have been treated by Damon (**1**) and Hughes (**3**), but both of them apparently attached little significance to the sporodochial habit. These two collections suggest an ontogeny from an initial absence of supernumerary cells through a hyaline vesicle state to a final multicellular, subfuscous condition. But it is noteworthy that the primary portion remains quite constant during these changes. Culture IMI



FIGS. 12–16. *B. moriforme*, conidia (12, 13, slide RTM I:207; 14–16, slide RTM I:226). FIGS. 17, 18. *B. minutissimum*, conidia. FIG. 20. *B. lingula*, conidium. FIG. 21. *B. granulosum*, conidium. Uniform magnification; scale in micra.

5805, which Hughes (**2**) says is very slow-growing, probably belongs here. His measurements are comparable, as are his figures 4D and 4F, including the furcate conidium, and figure 4A is almost certainly a sporodochium.

Material examined: NYS, on old decorticated apple wood, Sandlake (Buffalo), N. Y., TYPE. PAD (Saccardo coll.), on dead bark of *Vitis vinifera*, (Selva) Treviso, Italy, TYPE of var. *ampelinum*. (Slides RTM I:226, I:207 resp.)

Berkleasmium opacum nom. nov. FIGS. 7, 8

[1, *3*, *4*, *5*]

≡ *Sporidesmium opacum* Saccardo, Nuovo Giorn. Bot. Ital. **23**: 197. 1916. (Non *S. opacum* Corda, Icones Fung. **1**: 7. 1837.)

Material examined: PAD (Saccardo coll.), on dead wood of *Juglans cinerea*, Bolton, N. Y., TYPE, (slide RTM I:210). CUP (Atkinson coll. 1746), on oak (slide RTM I:235).

Berkleasmium triglochinis (Berk. & Br.) comb. nov.

[1, *3*, *4*, 5]

≡ *Sporidesmium triglochinis* Berkeley & Broome, Ann. Mag. Nat. Hist. IV. **17**: 141. 1876.

Berkleasmium vogelianum (Syd.) comb. nov. FIG. 19

[*1*, 2, 8]

≡ *Sporidesmium vogelianum* H. Sydow, Ann. Myc. **8**: 493. 1910.

Material examined: CUP (Syd. Myc. germ. exs. 947, ISOTYPE), on young fallen branches and peduncles of *Celtis occidentalis*, Brandenburg, Germany (slide RTM I:2).

SPECIES INQUIRENDA

Sporidesmium rauii Ellis & Harkness, Bull. Torrey Bot. Club **8**: 51. 1881. FIGS. 9–11

In accordance with the type description the conidia are light colored and the fructification tends to be intermediate between the tuberculariaceous and dematiaceous colony habits, *i.e.*, the spores tend to be grouped; the groups are sparse, linear to sporodochioid, of few to several conidia that may or may not be subtended by supernumerary cells. The colony morphology and hyaline conidia suggest an immature *Berkleasmium*, but the large size of the conidia precludes assigning it to any of the present species with comparable spore morphology.

Material examined: NY, on grape vine, Sallsburg, Penn., leg. *Rau*, TYPE (slides RTM I:247, S. C. Damon in QM).

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LITERATURE CITED

1. **Damon, Samuel C.** 1952. Type studies in *Dictyosporium, Speira,* and *Cattanea.* Lloydia **15**: 110–124.
2. **Hughes, Stanley J.** 1951. Studies on micro-fungi IV. Two fungi of *Betula* periderm. Comm. Mycol. Inst. Myc. Pap. **37**: 12–13.
3. ——. 1958. Revisiones Hyphomycetum aliquot cum appendice de nominibus rejiciendis. Can. Jour. Bot. **36**: 786.
4. **Moore, Royall T.** 1958. Deuteromycetes I: The *Sporidesmium* complex. Mycologia **50**: 686–688.

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Because of increased costs in labor, paper, presswork, etc., over the past five years, it is necessary to increase the price of reprints. Beginning with the January–February, 1960, issue of MYCOLOGIA the price of reprints will be as indicated on the inside back cover of this issue.

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